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ON THE STRUCTURE, FUNCTION, AND DISTRIBUTION OF THE PROLEGS OF THE PANORPOIDEA, WITH A CRITICISM OF THE BERLESE-IMMS THEORY.

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(Manuscript received 4th January, 1955.)
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With one Plate and 31 Text-figures.

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I. INTRODUCTION.

The material contained in this paper was first gathered together to form a section of a more general work on the evolution of the Panorpoidea. However, both because the structure and distribution of the prolegs is only of subsidiary importance in the study of the evolution of the Panorpoidea, and the amount of information available is so large, it has been decided to publish this section separately.

Since it is possible that my use of super-orders in the Endopterygota may not be clear to some readers who will therefore not know precisely what these

include, it seems best to list the orders under the super-orders accepted in this paper, as follows :

Super-order Neuropteroidea
1. Order Megaloptera
2. Order Neuroptera
3. Order Coleoptera
4. Order Strepsiptera

Super-order Hymenopteroidea
5. Order Hymenoptera

Super-order Panorpoidea (Panorpoid complex)
6. Order Zeugloptera
7. Order Trichoptera
8. Order Lepidoptera
9. Order Mecoptera
10. Order Siphonaptera
11. Order Diptera

Assumptions about the prolegs form much of the basis of the Berlese-Imms theory of development. These assumptions have not been adequately examined before, and this I have attempted to do in Section III.

II. THE PROLEGS OF THE PANORPOIDEA

A. Diptera

1. General Considerations.

The Diptera are dealt with here in considerable detail because they, more clearly than any other order, illustrate my contention that prolegs are secondary structures evolved *de novo* time and again to meet the specific requirements of the relation established between the larva and its environment. It is possible to assume with a considerable degree of confidence that the common ancestor of recent Diptera lived as a larva in liquid or semi-liquid decomposing vegetable matter (Hinton, 1947). In this environment it not only lost all trace of functional legs and any locomotory organs that it may have had on its abdomen, but its first instar lost all functional spiracles except those of the eighth abdominal segment.

It is not known to what extent the ancestral stock became differentiated into genera and families while in decomposing vegetable matter. In time, however, various groups successfully invaded other environments or became extinct. There is no conclusive evidence that any surviving Diptera have continuously retained the ancestral habitat although many have returned to it after lesser or greater periods spent in other environments. A continuous existence in the ancestral habitat of the order could only be doubtfully claimed for a very few nematocerous families, e.g. Trichoceridae and Anisopodidae and, even more doubtfully, Mycetophylidae, but all other groups that now occupy the ancestral habitat have clearly invaded it from other terrestrial or aquatic environments.

The larvae of no other order of insects are so diverse in structure and physiological requirements or have occupied so many different ecological

niches. It seems that the extraordinary adaptability of dipterous larvae owes its origin, at least to some extent, to the extreme simplicity established in their original habitat of decomposing vegetable matter, a simplicity of form and physiology that has been capable of being adapted to an enormous range of natural habitats. But this simplicity is of a special kind since simplicity of itself is not a promise of success, as recent apterygote insects, such as the Thysanura, bear witness. The simplicity of structure of the ancestral Dipteron is that of a highly complex animal that has become adapted and reduced in a special way and in a special environment that does not exclude by its own specialisations numerous other environments. For instance, the loss of legs in decomposing vegetable matter has not excluded an invasion of the soil or an endoparasitic life, both of which require relatively minor alterations in form from that evolved in decomposing vegetable matter. By contrast, it may be supposed that the possession of thoracic legs by a beetle larva is a great structural obstacle to an endoparasitic life, and that, other things being equal, the legless dipterous larva is much better equipped to invade such a habitat than is the beetle larva.

Detailed studies of the locomotion of some dipterous larvae have been made, but these will be published elsewhere since they are not relevant to my present purpose. In passing, however, it may be noted that in a large proportion of dipterous larvae there is no part of the body wall that is rigid, and, except for the head, there is no invaginated skeleton or system of phragma. This condition is approached by some other endopterygote larvae, especially caterpillars. In nearly all other active arthropods, however, a large part or even most of the body wall is rigid. In many adult beetles, e.g. Histeridae and Curculionidae, an extreme degree of rigidity and compactness is attained. Locomotion of these beetles is brought about by the action of numerous groups of antagonistic muscles and may be nearly correctly described in terms of the action of opposed muscles. In such beetles, the pressure of internal fluids can be said to affect but little the mode of locomotion, although even in these the levation of the claws appears to be effected only by the internal pressure, since, as in all other Antennata, the dactylopodite lacks the levator muscles present in the Chelicerata and Crustacea. *The importance of the pressure of the body fluids in locomotion and other body movements increases as the rigidity of the body wall decreases.* In most Cyclorrhapha the body wall is nowhere rigid, and thus the force developed by all the skeletal muscles is exerted against turgor pressure. Although in these larvae the skeletal muscles are so arranged that were the appropriate parts of the body wall rigid there would be many groups of antagonistic muscles, none actually function in this way, but in contraction all pull against a body wall that owes its rigidity to turgor pressure and not to its structure. It is evident that the locomotion of dipterous larvae is different in principle from that of the adults of the same species.

When describing the prolegs of different forms and the environments in which these structures have been evolved, it was felt desirable briefly to recount the chief structural and biological features of the larvae, a practice that has necessarily added to the length of this section but results in a clearer idea being conveyed to the reader of the plasticity of dipterous larvae and the specific circumstances that promote the development of prolegs.

Although I am not now concerned with the precise details of locomotion, it

should be said that apart from prolegs, generally present only in aquatic and subaquatic forms, other structures are locomotory in function, since all dipterous larvae move but only a few have prolegs. All dipterous larvae on damp surfaces or bound by a thin film of water to the substrate are able to crawl by suitable rhythmical contractions and extensions of the abdomen and also the thorax. When they are bound by a thin water film to a smooth surface, such as that of a glass plate, these movements appear to contribute more to their forward progression than do prolegs or other locomotory organs they may have. This type of locomotion is employed almost exclusively by a great many larvae. For instance, it is the chief means of progression of many Tipulidae and other larvae that have no locomotory setae or other locomotory organs on the ventral surface of the abdomen or thorax. In many species it may be the chief method of locomotion over dry surfaces. In others, such as many of the aphidiphagous Syrphidae that normally travel over dry surfaces, a liquid is secreted from the labial glands that may facilitate this type of locomotion by binding them to the surface so that all or nearly all of the muscular effort is expended in crawling and little or none in clinging to the substrate.

The most frequent and widely distributed organs that normally function only in locomotion are transverse welts. These are appropriately called creeping welts by many writers. Creeping welts are usually confined to the ventral surface of the segments on which they occur, but sometimes extend on to the sides. In some species creeping welts are present dorsally as well as ventrally. In others, the creeping welts are entire and completely encircle the segments. The welts are usually, but not always, armed with stiff setae or spines, usually curved, that are known as locomotory spinules. The stouter locomotory spinules do not differ in origin, structure, or function from the similar curved spines, called crochets, on the apices of most prolegs.

The pattern of the crochets or locomotory spinules on the creeping welts varies considerably. They may be evenly distributed over the welts or may be arranged in definite rows or patches. Sometimes, e.g. in many Mycetophylidae, there are two rows on the intermediate segments, the crochets of the anterior row being curved posteriorly and those of the posterior row being curved anteriorly. How one of these rows is thrown out of action when the larva moves forwards and brought into action when it moves backwards, has still to be investigated. No comparative studies have been made of their form and distribution or of their function in locomotion. Rows and patches of locomotory spinules of various kinds are present in some larvae on segments where there is no raised area that can be called a welt. Sometimes locomotory spinules are present on the dorsal surface. In *Vermileo* (Rhagionidae) which crawls on its back, there is a transverse row of such spinules on the dorsal surface of the seventh abdominal segment.

The creeping welts of a large number of different larvae have been examined, and in every one muscles were found to be inserted. The degree to which the creeping welts are retracted and protracted during locomotion varies greatly. In many species it was found that they were more retractile than some prolegs. The welts are usually distinctly transverse and extend from one side to the other across the middle of the segment. Apart from their shape, they differ in no important structural feature from prolegs. In some

larvae, e.g. species of *Tabanus*, the creeping welts may be subdivided to form oval and more or less sharply delimited projections that cannot be distinguished satisfactorily from prolegs; and a study of the Tabanidae leaves no room for doubt that one way in which prolegs have arisen is by modification from creeping welts.

On a structural basis no sharp line can be drawn between creeping welts and prolegs, and anyone who maintains that prolegs are serially homologous to thoracic legs must also allow a similar homodynamy for creeping welts. Structures do occur that are so intermediate between creeping welts and prolegs that they can only be placed arbitrarily in one or other of these categories. Nevertheless, the distinction between the two is a real one that is particularly evident when these structures are not viewed in isolation from the specific differences in the environments in which they are evolved.

Distinct sucking organs used both in fixing the larvae to the substrate and in crawling are present in the Psychodidae and Blepharoceridae. In the latter family they are invariably present and are particularly well formed (fig. 7). In addition to distinctly formed sucking organs that maintain their integrity, many larvae when moving on a wet surface develop, by contraction of the appropriate muscles, temporary sucking organs on the ventral surface of the abdomen and sometimes also the thorax. On wet surfaces temporary sucking organs are developed in most larvae that I have seen that have a relatively smooth and thin cuticle. A temporary sucking organ is formed when the central part of an area of the body wall in contact with the substrate is lifted by muscular action in such a way that the peripheral region remains in contact and is sealed by a film of water or other liquid.

In most Brachycera-Cyclorrhapha, and probably in most Brachycera-Orthorrhapha, the mandibles play an important part as accessory locomotor organs. The mandibles of these are directed downwards, and, as the larvae move, are continually thrust against the substrate. When the mandibles are held in an irregularity of the surface, the larva can draw itself forwards by contracting the appropriate muscles. The mandibles then release their hold, the body is extended, and, when the mandibles again secure a purchase on the surface, the process is repeated. In certain situations, such as when climbing, the mandibles of some species may function as the chief locomotory organs, but in most circumstances their rôle in locomotion is only subsidiary. It is this use of the mandibles that chiefly accounts for their wearing down, particularly at the end of the final instar, which is usually the instar of longest duration. The wearing down of the mandibles of *Tabanus* and other larvae has occasionally been noticed by writers. Some larvae, e.g. the first instar of *Pterodontia* (Acroceridae) move in a series of loops like a leech (King, 1916). These attach themselves by their mandibles and then draw up the anal disk to the head. When the anal disk is firmly attached, the mandibles are released and the body is extended. They then attach themselves to a new forward position with their mandibles and the process of bringing up and attaching the anal disk is repeated. The larvae of some Phoridae apparently move in the same way. According to Keilin (1915 : 42), " Les larves de *Phora* servent de leur bouche comme d'une ventouse et elles rampent à la manière des sangsues ". It is possible that the pre-oral cavity of *Phora* is being used as a sucker.

The larvae of some Nematocera also use their mandibles in locomotion, e.g.

Anisopus Meig. and *Mycetobia* Meig. (Anisopodidae). Of the Anisopodidae Keilin (1915 : 42) says, " La larve peut produire, par ces mandibules, des mouvements rapides et alternatifs, dans le plan vertical, en les appuyant contre le support, tout à fait à la manière des pattes ; cela produit un déplacement rapide de tout les corps de la larve, qui reste tout à fait inerte. Les mandibules ont ici une forme spéciale qui est en rapporte avec leur fonction ".

A number of unrelated dipterous larvae are able to jump in various ways. The best known of these are the Piophilidae and particularly the cheese-skipper, *Piophila casei* L. According to Wille (1923), *P. casei* does not leap until the fifth day of its six days of larval life. When about to leap the larva forms a vertical loop by bending its head backwards and underneath its abdomen until the mandibles engage a transverse fold near the spiracles of the last segment[1]. The longitudinal muscles on the outer side of the loop are then contracted, and, when the mandibles are released, the larva is thrown into the air for a height of up to 20 cm. Some Clusiidae leap in a similar manner (Keilin, 1915) as also do some Trypetidae such as the mature larva of the Mediterranean fruit-fly, *Ceratitis capitata* Wied. (Woglum, 1929). A large number of Cecidomyiidae jump in a somewhat similar way, as was first shown by Winnertz (1853), but in this family hooks on the last abdominal segment engage a strongly sclerotised, usually spatulate and bifid, projection beneath the prothorax. In the Cecidomyiidae the anal hooks are thus the functional equivalent of the mandibles of the Piophilidae, Clusiidae, and Trypetidae. According to Kieffer (1913), Cecidomyiid larvae also form a loop perpendicular to the surface, and by unbending like a tense spring are thrown to a distance of several centimetres. He records the habit in fifteen genera, and since his paper (1913) many other genera have been found to have anal hooks and a prosternal projection. Other observations on the jumping larvae of the Cecidomyiidae are given by Chaine (1913).

The free-living first instar larvae or planidia of the Acroceridae (= Cyrtidae) jump in two very different ways. The species of *Pterodontia* Gray attach themselves to the substrate by their perianal region so that they are perpendicular to the surface. In this position two long posterior setae are at right angles to the long axis of the body. By a sudden downward thrust of these setae, which brings them into line with the long axis, the larva is projected 5–6 mm. into the air (King, 1916). The species of *Oncodes* Latr. fix their body perpendicularly to the surface in the same way, but the posterior setae are short and do not function in jumping. From this erect position the body is looped so that the mandibles (?) engage short curved hooks near the anus. The dorsal longitudinal muscles are then probably contracted. When the anal hooks are released, the violent straightening movement projects the larva into the air (Bovey, 1936).

[1] In the larvae of *P. casei* that I have observed the mandibles usually engage the ridge between the two papillae on the middle of the hind margin of the eighth segment, these papillae being folded forwards and inwards when the body is looped. Sometimes, however, the mandibles engage the raised border lateral to the papillae. On a smooth surface, e.g. on a glass plate, the loop formed is horizontal and not perpendicular to the surface. When the loop is formed on a smooth surface, the initial movements in its formation not only consist of moving the head posteriorly beneath the body, but the apex of the abdomen is also bent beneath and brought forwards to meet the head.

According to Wheeler (1931), both young and mature larvae of *Vermileo* Macq. (Rhagionidae) are able to leap. When the larva is taken out of its pit, it lies on its side with its body bent S-shaped. Its leaping movements consist of two phases "a sudden, violent contraction of antagonistic muscles producing a complete reversal of the S-shaped flexure of the body, and as sudden a return to the original position. Though the larva is lying on its side, the first contraction throws it off the substratum, and the second occurs in the air or just as it is landing".

2. Independent evolution of prolegs in dipterous larvae.

The evidence for the independent origin of the prolegs in the various groups is discussed below under the headings of the families to which they belong. Within the Diptera prolegs have been independently evolved in at least 27 groups, as follows:

Dixidae	1
Chironomidae (+ Ceratopogonidae)	1
Thaumaleidae	1
Simuliidae	1
Blepharoceridae	1
Deuterophlebiidae	1
Tanyderidae	1
Ptychopteridae	1
Tipulidae	1
Rhagionidae	2
Tabanidae	1
Therevidae (+ Scenopinidae)	1
Asiloidea	1
Empididae	1
Dolichopodidae	2
Syrphidae	1
Ephydridae	1
Canaceidae	1
Sciomyzidae	1
Calliphoridae	1
Muscidae	5
Total	27

When dipterous larvae are better known the number of groups that have independently evolved prolegs will undoubtedly be found to be much greater than 27. The number of times that prolegs themselves have been independently evolved is, of course, very much greater than 27.

In some Tabanidae, for instance, there are no less than four series of prolegs, and each of these series is almost certainly evolved at a different time during the evolution of the group, as may be seen from a study of the dorsal pairs. A study of the dorsal and sublateral pairs, not only in the Tabanidae but also in the Asilidae, clearly shows that all the prolegs of a series do not arise simultaneously. Therefore, not only are the prolegs of the different series

evolved at different times, but, with the possible exception of the pairs of the most ventral series, many of the pairs within each series are also evolved separately in time.

The Tabanid with the greatest number of prolegs is *Tabanus kingi* Aust., which has 57. This species has four pairs on each of the first seven abdominal segments and a single ventral proleg on the eighth. The latter proleg appears to have been evolved as an unpaired median structure from the preanal creeping welt after the ancestor of *T. kingi* invaded fast-flowing streams. Even assuming that each series of prolegs in the Tabanidae was evolved but once, i.e. that the species with eight prolegs on a segment were evolved but once from those with six, those with six but once from those with four, and so on, prolegs have clearly been evolved on at least five separate occasions in the family. But, as already noted, the pairs of the dorsal and lateral series do not always arise at the same time, and therefore prolegs have been independently evolved many more than five times in the Tabanidae. Not including the ventral series, there are a maximum of 21 pairs of prolegs in the Tabanidae, and it appears likely that a high proportion of these pairs were evolved at different times during the evolution of the family, although it is possible that the ventro-lateral series was evolved *en bloc*, as probably was the ventral series at an earlier period.

3. The relation of prothoracic prolegs to feeding habits.

Table I shows the great variation in the number and position of the prolegs in the Diptera. Prolegs are never present on the meso- and metathorax. It is true that in a few Syrphids, e.g. *Ferdinandea cuprea* Scopoli, prolegs are said to be present on the mesothorax, but I have little doubt that further study of these will show that the first pair of prolegs is actually on the prothorax.

Prolegs are present on the prothorax of some free-living phytophagous and saprophagous groups, but are very nearly always absent on the prothorax of predaceous species. This relation between structure and feeding habits not only obtains between families but also between groups within a family. For instance, in the Syrphidae the Eristalinae, Chilosiinae, Milesiinae, and other saprophagous forms have a pair of crochet-bearing prolegs on the prothorax, but the predaceous species, such as the Syrphinae, never have thoracic prolegs although many have rudimentary prolegs on the abdomen. *Metasyrphus luniger* Meig. and *Sphaerophoria flavicauda* Zett. have, according to Bhatia (1939), numerous papilla-like locomotory swellings that are confined to the abdomen.

The existence of a relation between thoracic prolegs and feeding habits makes it possible sometimes to predict the feeding habits of particular species. The presence of prolegs on the prothorax appears to be a good indication that the species is not predaceous, although their absence provides no clue as to feeding habits. It may be supposed that any fleshy projection near the head of a predator might afford a purchase or an effective point of attack to the species being attacked and that this disadvantage outweighs any selective value prolegs near the head might have in locomotion. In this connection it is interesting to note that even creeping welts tend to be absent on the prothorax of predators. A few Chiromidae (Pelopiinae) are predaceous and have well developed prothoracic prolegs. This may be evidence that their predaceous habits are of relatively recent origin.

TABLE I.—*The number and distribution of prolegs in various groups of the Diptera.*

	Thorax.			Abdomen.										Total.
	I	II	III	1	2	3	4	5	6	7	8	9	10	
Dixidae	.	.	.	2	2	.	.	.	.	.	.	.	.	4
Chironomidae	1–2	.	.	.	.	.	.	.	.	.	.	.	1–2	2–4
Ceratopogonidae	0–2	.	.	.	.	.	.	.	.	.	.	1–2	.	1–4
Thaumaleidae	1	.	.	.	.	.	.	.	.	.	.	1	.	2
Simuliidae	1	.	.	.	.	.	.	.	.	.	.	1	.	2
Blepharoceridae	.	.	.	.	2	2	2	2	2	2	.	.	.	12
Deuterophlebiidae	.	.	.	2	2	2	2	2	2	2	.	.	.	14
Tanyderidae	.	.	.	.	.	.	.	.	.	.	2	.	.	2
Ptychopteridae	.	.	.	4	4	4	2	2	.	.	.	.	.	16
Tipulidae (*Dicranota*, etc.)	.	.	.	.	.	2	2	2	2	2	.	.	.	10
(*Pedicia rivosa* L.)	.	.	.	.	.	.	2	2	2	2	.	.	.	8
Rhagionidae (*Atherix*)	.	.	.	2	2	2	2	2	2	2	2	.	.	16
(Vermileoninae)	.	.	.	1	.	.	.	.	.	.	.	.	.	1
Tabanidae (*Chrysops*)	.	.	.	4	4	4	4	4	4	4	.	.	.	28
(*Tabanus*)	.	.	.	6	6	6	6	6	6	6	.	.	.	42
Ditto	.	.	.	6	8	8	8	8	8	8	.	.	.	54
,,	.	.	.	8	8	8	8	8	8	8	.	.	.	56
(*T. kingi* Aust.)	.	.	.	8	8	8	8	8	8	8	1	.	.	57
Asilidae (*Lasiopogon*)	.	.	.	2	2	2	2	2	.	.	.	.	.	10
(*Leptogaster* sp.)	.	.	.	.	2	2	2	2	2	2	.	.	.	12
(*Dioctria* sp.)	.	.	.	2	2	2	2	2	2	.	.	.	.	12
(*Cryptopogon* sp.)	.	.	.	2	2	2	2	2	2	2	.	.	.	14
(*Laphyria flava* L.)	.	.	.	6	6	6	6	6	6	.	.	.	.	36
(*Laphyria* sp.)	.	.	.	6	6	8	8	8	8	.	.	.	.	44
(*Laphyria* sp.)	.	.	.	6	8	8	8	8	8	.	.	.	.	46
(*Laphyria gilva* L.)	.	.	.	8	8	8	8	8	8	.	.	.	.	48
Empididae (*Hemerodromia*)	.	.	.	.	2	2	2	2	2	2	2	.	.	14
(*Roederiodes*)	.	.	.	2	2	2	2	2	2	2	2	.	.	16
Syrphidae (many spp.)	2	.	.	2	2	2	2	2	2	.	.	.	.	14
Ephydridae (*Ephydra*)	.	.	.	2	2	2	2	2	2	2	2	.	.	16
Muscidae (*Limnophora*)	.	.	.	.	2	2	2	2	2	2	2	.	.	14
(*Graphomyia*)	.	.	.	.	2	2	2	2	2	2	.	.	.	12

4. The relation of prolegs to environment

From the distribution of prolegs in the larvae of the Diptera, it is clear that retractile, crochet-bearing prolegs tend to develop only in species that are aquatic or subaquatic. The evidence for this is discussed in detail under the family headings. Except for a few groups, sufficient evidence is available to show beyond much doubt that the terrestrial species that have prolegs are in fact derived from aquatic forms. The evidence suggests that the ancestors of these terrestrial species evolved prolegs while in aquatic or subaquatic environments and that probably the invasion of a terrestrial environment is still sufficiently recent for the prolegs not to have been lost.

The superfamily Asiloidea appears to constitute the most striking exception to the rule that in the Diptera prolegs are evolved only in aquatic or subaquatic environments. The total lack of independent evidence for an aquatic origin of the ancestor of the superfamily is discussed below under the heading of the family Asilidae.

The structure and distribution of the prolegs in the Asiloidea does suggest

an aquatic origin for the group, but it must be clearly understood that this suggestion is made only because nearly all other larvae with prolegs have evolved these structures in aquatic or subaquatic environments. A hypothesis of this kind is legitimate, but, of course, the existence of prolegs in the Asiloidea, which are therefore presumed to be aquatic in origin, cannot be used to support the generalisation previously made of the relation between prolegs and environment without indulging in a circular argument.

Two groups of larvae are known to me that have prolegs that were apparently evolved in a terrestrial environment. In the Rhagionidae there is a single mid-ventral proleg on the first abdominal segment of all known species of the Vermileoninae, the " worm-lions " that live in pits in dust or sand. The chief function of this proleg appears to be to assist the larvae, which rest ventral surface uppermost, to hold their prey. There seems to be little doubt that this proleg was evolved in a terrestrial environment, and that it is an exception to my generalisation that prolegs tend to be evolved only in aquatic or subaquatic environments. For further comments and a reply to Wheeler's (1931) suggestion as to the origin of this proleg see p. 485.

The related families Therevidae and Scenopinidae that have a pair of ventral prolegs on the apex of the last abdominal segment constitute the other certain exception to my generalisation that prolegs tend to be evolved only in aquatic or subaquatic environments. The function of the prolegs in the Therevidae and Scenopinidae has not been studied, but they probably assist in locomotion.

Larvae living in liquid or semi-liquid vegetable and animal matter characterstically lack creeping welts and prolegs, terrestrial larvae usually have creeping welts but no prolegs, and free-living aquatic larvae that do not normally move by swimming, as do the Culicidae, have retractile prolegs that are usually armed with crochets. At first sight it might be supposed that the difference in locomotion and locomotory structures between the larvae living in liquid or semi-liquid organic matter, on the one hand, and those living in aquatic or subaquatic environments, on the other, might be attributed simply to a difference in the viscosity of the two environments. Looking at the matter a little more closely, however, it is apparent that it is not primarily a difference in the viscosity of the medium that accounts for the differences observed between the two groups of larvae.

In their actual occurrence in nature, environments of decomposing organic matter that are more viscous than water differ in two important particulars from aquatic environments. Firstly, there are usually no firm supports running through the medium, whereas in aquatic environments the water plants are firm supports on which the larvae can crawl through the water. Secondly, the oxygen tension in decaying organic matter is much lower than in normal aquatic environments.

Owing to the second of these factors, the relative lack of oxygen, larvae in liquid organic matter are confined to a position relatively near the surface or can penetrate to the lower levels only for short periods of time before they are forced to come again to the surface to take in another supply of air. Even near the surface, cutaneous respiration does not suffice, and larvae in such environments never become apneustic, although a contributory factor in the retention of at least one pair of functional spiracles is the relative impermanence of these environments.

Environments of liquid organic matter have a firm substrate like aquatic environments, but lack of oxygen at the bottom precludes larvae from using the substrate for locomotion ; and they are in fact, in deep mature environments of this type, confined to the upper levels where they may supplement their oxygen requirements by cutaneous respiration but in any case have easy access to the surface. Now it is precisely the upper levels of such environments that are the most liquid and contain the fewest animal and plant remains that can be used for support by a crawling larva.

The Syrphidae constitute the only exception at present known to me of the rule that dipterous larvae living in liquid organic matter lack prolegs. Many Syrphid larvae have secondarily invaded environments of liquid or semi-liquid organic matter from aquatic environments in which their ancestors evolved prolegs and a respiratory syphon. They are relatively large larvae that normally do not live at depths greater than those corresponding to the lengths of their respiratory syphons. It appears, therefore, that the prolegs of Syrphid larvae are retained precisely because they are advantageous in crawling on the substrate, which they are capable of doing because their respiratory syphons make them independent of the oxygen tension of the bottom levels.

Larvae that swim effectively in liquid organic matter swim but poorly when placed in water. In liquid organic matter they obtain points of support for their backward thrusts by compacting loose strands and other debris ; and the movements required to do this effectively are not the same as those required in water. The waves of contraction that pass posteriorly do not materially alter the length of the swimming larva, its length being maintained by a combination of the turgor pressure and the elasticity of the cuticle. The movements of such larvae in liquid organic matter are more nearly like those of nematodes that live in similar environments. An apparent exception may be noted : some of the eel-like, prognathous genera of Ceratopogonidae live in open water in lakes and rivers. Nevertheless these swim poorly, and in open water they are usually to be found about floating algae, amongst the strands of which their movements are very effective.

In addition to the species with functional spiracles that live in more or less liquid organic matter under anoxic conditions, some apneustic Ceratopogonids live in liquid organic matter like oozing sap of injured trees. It may be supposed that such environments are comparatively better aerated. I have never found apneustic larvae that lack haemoglobin in more or less anoxic organic matter, although it may be supposed that in such environments some might survive if they maintained themselves near the surface.

5. Family characteristics.

(i) *Dixidae.*

Only two genera and about 100 species are known in this family. *Dixa* Meig. is cosmopolitan, and the peculiar method of locomotion of its larva has attracted the attention of several observers since it was first described by Réaumur in 1714. The larvae, which are metapneustic, feed on plankton and algae and other small organisms caught beneath the surface film. They normally live above the general water level on wet stones and sticks in streams.

Although at first sight they appear to be living above the surface, most of the body is below the surface film. In *Dixa nebulosa* Meig. the dorsal caudal processes and dorsal plates on abdominal segments 2–7 are fringed with hydrofuge hairs that attach the larva to the surface film so that at rest or when crawling only the dorsal parts of segments 2–7 of the abdomen are exposed to the air.

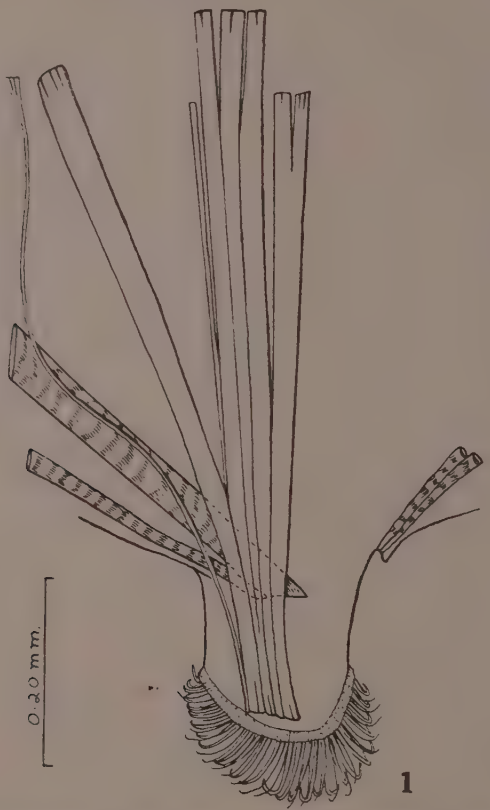

Fig. 1.—*Dixa nebulosa* Meig., mature larva. Outer view of proleg of left side of first abdominal segment. Retractors of proleg unshaded and basal muscles shaded.

There is a pair of ventral, retractile, crochet-bearing prolegs on each of the first two abdominal segments. These prolegs are not dorsal as is sometimes claimed, e.g. Malloch (1917). The proleg musculature is shown in fig. 1. In *Dixa nebulosa* Meig., and at least in some other British species of the genus, there is a prominent transverse welt on the middle posterior margin of the seventh segment. This welt might be held to be a median proleg. It is densely and finely setose. Similar but much less prominent welts are present near the posterior margin of segments three to six.

The body at rest is held so that it is ∩-shaped, the third and fourth segments forming the bend. When it moves it retains its ∩-shape, and the bend of the ∩ is convex in the direction of movement. The larva begins to move by pushing forwards with its prolegs while the hind end of the body is prevented from slipping by a row of stout caudally directed spines on each side of the median line near the posterior margin of segments five to seven. The transverse welts of the posterior segments probably also function to prevent backward slipping. The principal second movement is to bring the caudal end of the body forwards while the thorax and first two abdominal segments are prevented from slipping by the paired prolegs. The completion of this movement re-establishes the bend in its original position relative to the cephalic and caudal halves. These two principal movements are executed alternately, and at times the larva gives the impression of moving with considerable speed. It should be noted that the forward displacement of the ∩-shaped larva is effected by the caudal half moving forwards and the anterior half moving backwards in the sense that it is moving away from the direction in which the head is pointed when horizontal. The larva may have the anterior half of the body to the right or to the left of the posterior half, and no obvious difference in the speed of movement in either of these positions has been noted.

The surface film binds the larva to the substrate. This means that on inclined or vertical surfaces its energy is not expended on clinging but can be actively employed in pushing its body forwards.

The Dixidae are very closely related to the Culicidae, and they are frequently given no more than subfamily rank within the latter family. No Culicidae have prolegs on the anterior abdominal segments, and there is no evidence to suggest that the prolegs of the Dixidae are not independently acquired after the separation of their ancestor from the common ancester of the Dixidae and Culicidae.

(ii) *Chironomidae* (= *Tendipedidae*).

The Chironomidae are one of the largest families of nematocerous Diptera. The larvae of the great majority live in standing or running freshwater, but some (e.g. some Clunioninae) are marine and a few are terrestrial. They feed chiefly on algae, diatoms, and decaying vegetable matter, but a few are predaceous. All are apneustic, and recent terrestrial forms are derived from aquatic ancestors and remain apneustic.

In apparently all freshwater and marine forms there is a ventral proleg on the prothorax with muscles as shown in fig. 2. This proleg is more or less distinctly cleft apically, according to the species. It has almost certainly been evolved from the fusion of two separate prolegs, and in all forms examined retains two distinct sets of muscles, these being retained even in those species in which it is hardly noticeably cleft apically. In many species the apical cleft is deep, and there are two distinct and separate prolegs united proximally but each having its own system of apical crochets or stiff hairs. The prolegs of the latter species are thus paired structures not distinguishable in gross external form from the paired prothoracic prolegs, also united proximally, of many Ceratopogonidae.

There has been some dispute as to the number of abdominal segments, some

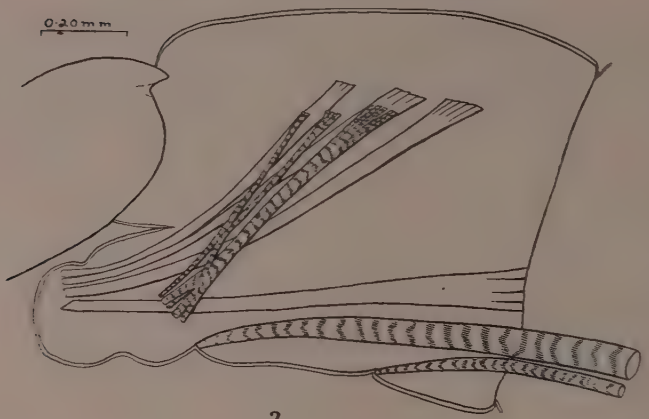

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FIG. 2.—*Chironomus plumosus* L., mature larva. Left side of prothoracic proleg. Retractor muscles unshaded and basal and other muscles shaded. The two ventral muscles extend through the prothorax and arise on the hind margin of the mesothorax.

writers claiming nine and others ten. The latter view is held by Zavrel (1918) and others, and it is supported by my own studies of the external structure and musculature, but the number of abdominal segments, whether nine or ten, or even eight (Malloch, 1917), is not strictly relevant to my present purpose. In all freshwater and marine species there are two ventral prolegs on the tenth segment, each bearing large and conspicuous crochets (fig. 3).

The terrestrial species live among grass roots, in moss, in decaying vegetable matter, and in manure. In the North American species of *Camptocladius* Wulp, a terrestrial genus, the prothoracic prolegs are poorly developed and the anal prolegs are fused "in the form of a single sessile disc whose margins are furnished with small hooks" (Malloch, 1917 : 288). In an unidentified terrestrial British species that I have examined the anal prolegs are well-developed and not fused, but the prothoracic prolegs are much reduced and completely retractile. Other similarly modified terrestrial species have been described by Lenz (1923) and Thienemann and Kruger (1939).

The fact that all Chironomidae are apneustic and that all but a few evidently specialised genera live in freshwater is sufficient evidence that the ancestors of those that are now marine or terrestrial were freshwater forms. The prolegs of both the prothorax and tenth abdominal segment are well developed in apparently all freshwater and marine forms. The noticeable reduction of one or both pairs of prolegs in terrestrial forms is evidence of the clearest kind of the connection between prolegs and an aquatic habitat.

(iii) *Ceratopogonidae* (= *Heleidae*).

Most Ceratopogonid larvae are predaceous, but some, e.g. *Forcipomyia* Meig., feed on moulds, fungi and decomposing vegetable matter. All known species are apneustic in all instars, and Keilin (1944) and Hinton (1947) for this reason believe that the larvae are primitively aquatic. Malloch's (1917 : 282)

claim that some are metapneustic is incorrect. Independent (if the thesis developed in this paper is correct) but less conclusive evidence that they are primitively aquatic is found in the distribution of the prolegs within the family.

The larvae live in three different environments. Many are aquatic, some are terrestrial, e.g. *Forcipomyia*, and others, such as species of *Dasyhelia* Kieff. and *Culicoides* Latr., live in semi-liquid or liquid vegetable matter and are commonly

FIG. 3.—*Chironomus plumosus* L., mature larva. Left proleg of the tenth abdominal segment. The retractor muscles of the proleg and of the appendage of the ninth abdominal segment are unshaded. Of the four groups of retractor fibres, 1 has its origin at the median line just above the inner base of the proleg, and groups 2–4 originate in the ninth segment. Of the latter, group 4 of the left proleg crosses over group 4 of the right proleg and has its origin on the right side of the ninth segment. Similarly, group 4 of the right proleg originates on the left side of the ninth segment.

found in sap oozing from wounds in elm and other trees. The latter are sometimes spoken of as terrestrial, but the matrix in which they live is liquid, and the adaptive structural modifications undergone by insect larvae in such a matrix are similar in certain respects, e.g. reduction in number of functional spiracles, to those that take place in water. But the effect on prolegs and legs of liquid or semi-liquid organic matter differs greatly from the effect of water: in the former they are relatively quickly lost, whereas in water legs are never lost and prolegs are developed or preserved but never lost.

It appears probable that the Ceratopogonidae may have arisen from the same ancestral stock as the Chironomidae either before or after the larva of their common ancester had become aquatic. In water the larvae became apneustic in all instars and developed a pair of ventral prolegs on the prothorax and one or two prolegs on the ninth abdominal segment. In some, including species of *Forcipomyia*, the ninth abdominal segment has a single transverse proleg bearing crochets ; and there is no clear evidence that the appendage of this segment first arose as a paired structure.

The secondarily terrestrial species (*Forcipomyia* Meig., *Thyridomyia* Saund., etc.) have well developed prothoracic and anal prolegs which were almost certainly evolved before the ancestors of the recent species quit the water. In *Forcipomyia* (s.str.) paired, usually spatulate, setae on the head, thorax and abdomen secrete a substance that extracts water from the atmosphere. The solution is supposed by Keilin (1918) to run down the setae and moisten the cuticle. An hygroscopic film over the cuticle, which must be relatively permeable since it must be permeable to air, will not, of course, prevent the internal fluids from reaching equilibrium in time with an atmosphere of lethal relative humidity, but such a film will serve as a temporary buffer and enable the larvae to survive short exposures to relative humidities which would otherwise have killed them. Keilin's theory of the function of the spatulate setae is, however, entirely incorrect : they are defensive in function. An account of experiments that show this will be published shortly.

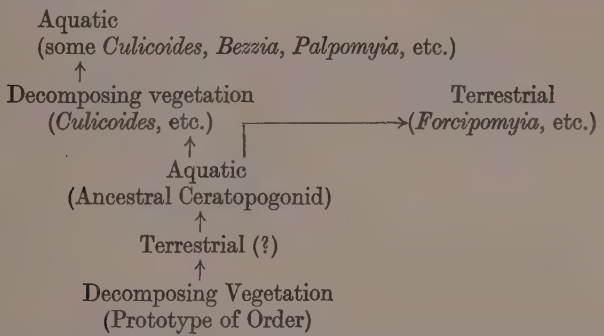
Among the aquatic species two very distinct types are found : short and relatively broad species with prothoracic and anal prolegs or only with anal prolegs, and long and very narrow species that lack prolegs. Species of the first group are usually somewhat flattened, whereas those of the second group are round in cross section. The head is always prognathous in the eel-like species without prolegs, but it is also prognathous in some aquatic genera with both thoracic and anal prolegs, e.g. *Apelma* Kieff. that lives in the capillary water between the leaves of terrestrial Bromeliads. In *Apelma* the apices of the mandibles move in a sagittal plane (Saunders, 1925), as they do in all hypognathous genera that I have examined. Some of the broad forms, e.g. at least some *Dasyhelia*, are found in elm-tree wounds and lack prothoracic prolegs (Johannsen, 1937). The latter thus exhibit an apparently significant correlation of habitat and structure, and it appears reasonable to assert that the prolegs evolved in water are now in the process of being lost in an environment in which such appendages are usually lost, whatever the group, as their functional use is below that necessary to retain their selective value.

The genera with a long, narrow, eel-like body more or less round in cross-section progress by eel-like wriggling movements ; and some of these (e.g. some *Culicoides*, *Palpomyia* Meig., etc.) are frequently found in oozing tree wounds and liquid or semi-liquid vegetable matter. Their speed of movement in these environments is in marked contrast to that of the broad forms like *Dasyhelia*. But the eel-like forms are not restricted to semi-liquid or liquid vegetable matter: they are frequently found amongst algae in water, e.g. *Bezzia*, Kieff. *Probezzia* Kieff., and some *Culicoides*.

The only known free-swimming legless insect larvae are those of the Culicidae ; and these without exception have anal fins, appendages possibly evolved from prolegs. The eel-like aquatic Ceratopogonidae swim moderately effectively

in the water, but I do not think it at all likely, though not impossible, that their form was evolved in the water : to believe the contrary it is necessary to believe that their ancestors lost their prolegs while in the water, a circumstance without parallel in insect larvae unless it can be shown that the anal fins of the Culicidae are not much modified prolegs.

The available evidence seems to indicate that the primitive Ceratopogonid larva was short, had both prothoracic and anal prolegs, and a prognathous head with mandibles moving in a horizontal plane. Some of these became terrestrial and still retain their prolegs, whereas others left the water for liquid of semi-liquid vegetable matter where, in time, their prolegs were lost (an intermediate stage in this process is exhibited by some recent species of *Dasyhelia*) and their bodies became eel-like. Some of the eel-like species again became adapted to water, perhaps owing to the frequent flooding of their environment, and their new method of locomotion was sufficiently effective in water not to stimulate a further change in body form. The argument developed here may be diagrammatically expressed thus :



To the claim that *Culicoides* and allied genera have retained the habit of living in decomposing vegetation and have never had a long aquatic history we can oppose the fact of their apneustic respiratory system. The last instar is apneustic and therefore all previous instars are apneustic, according to my second rule of reduction (Hinton, 1947). The number of functional spiracles is usually reduced in liquid or semi-liquid vegetable matter, but in no known case are all functional spiracles lost in the final instar. That some spiracles will be retained in a functional condition in the final instar follows from the fact that in nature such environments are poor in oxygen and do not endure but are subject to frequent desiccation. The Mycetophylidae are a very numerous group living in decaying fungi, but no fungivorous species is apneustic in its final instar. The only insects that have become apneustic in a terrestrial habitat are Mycetophylids that have left fungi and that now live invested in an hygroscopic film ; they are the exceptions that prove my rule that it is only an aquatic environment that leads to the development of an apneustic system in a final instar larva.

The musculature of the prothoracic prolegs of *Forcipomyia* (fig. 4) has been accurately described by Saunders (1924). Each proleg has three distinct groups of muscles : (1) three apical retractors that arise on the tergum of the pro-

thorax; (2) a single median muscle arising on the postero-ventral margin of the prothorax and inserted on the base of the proleg; and (3) two muscles also inserted on the base but passing through the prothorax and mesothorax and arising on the postero-ventral margin of the latter segment. The muscles of the prothoracic proleg of *Atrichopogon* Kieff. are described by Nielsen (1951). The anal proleg or prolegs have apical retractor muscles, and these prolegs, like the prothoracic, are exserted only by blood pressure.

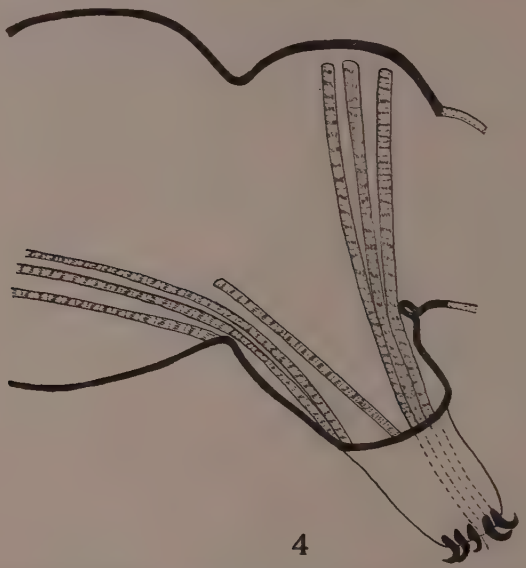


Fig. 4.—*Forcipomyia bipunctata* L. Right proleg of prothorax as seen from right side (after Saunders, 1924).

The locomotion of *Apelma* has been briefly described by Saunders (1925 : 258) as follows: "These hooks [crochets of anal prolegs] come into use when the larva wishes to move fast, the procedure being interesting and unusual owing to the confined space [capillary water between Bromeliad leaves] in which it lives. The posterior end of the body is bent to one side until the extremity of the body is about on a line with the middle of the body; the larva then grips the substratum with its posterior pseudopod and straightens itself, thrusting the body forward, while the extremity of the abdomen makes a half turn, pivoting upon its temporary point of attachment".

When *Forcipomyia* is allowed to crawl upside down on a moistened glass plate, the thoracic prolegs are usually only partly extruded so that their apices are concave and function as minute vacuum cups. In such circumstances another small vacuum cup is often formed below the cleft on the posterior side of the common base, but there is no regularity about this, and a temporary sucker may be formed on one side or half way up a proleg, these irregularities owing their origin to variations in the angle of contact with the surface and

variations in the local temporary equilibrium between muscle contraction and turgor pressure. The perianal region is also frequently used as an adhesive organ and less frequently the sternal region of the sixth and seventh abdominal segments. If the surface of the glass has a slightly thicker film of water, the middle of sternites 2–9 or even 1–9 appear sometimes to function as temporary suckers.

(iv) *Thaumaleidae.*

Only a few species and four genera of Thaumaleidae have been described. The larvae live on stones and sticks in clear streams and feed on diatoms and other algae. As a rule they are found only on wet surfaces or where the water is running very thinly over the surface. At such times the lower half of the body up to the level of the lateral setae, the head, and all of the ninth segment and posterior proleg are below the surface, the top half of the body being exposed to the air. Even when the larvae are washed into the stream, the top half of the body usually remains dry, and the two pairs of functional spiracles (S_1 and S_8) remain exposed above the surface.

The locomotion of *Thaumalea testacea* Meig. has been described by Thienemann (1909). My own observations show that, when not strongly stimulated, *Thaumalea* moves with the body straight or almost so, using the anterior proleg for propulsion. At such times the posterior proleg is usually not or only little used for backward thrusts, being usually partly retracted so that the crochets do not catch in the substrate. The posterior proleg is used to anchor the larva to the substrate. The musculature of the anterior proleg is shown in fig. 5.

The systematic position of the Thaumaleidae is not definitely known. At one time they were included in the Chironomidae, but they bear only a superficial resemblance to this family; the larvae are amphipneustic instead of apneustic, the caudal proleg is unpaired, the mouthparts are very different, the head is hypognathous instead of prognathous, and the pupa (Saunders, 1923) is peripneustic instead of propneustic. In some ways they resemble the Ceratopogonidae, but their amphipneustic larvae preclude a derivation from the latter family.

(v) *Simuliidae.*

The larvae of the Simuliidae are plankton feeders living in running water, and they are particularly abundant in fast-flowing streams of temperate and tropical regions. One species is known to inhabit the littoral of lakes in Africa. The larvae are all very similar, and as late as 1906 all were placed in the genus *Simulium*. A number of different genera are now accepted, but these are chiefly based on differences in adult structure. The Simuliidae are an isolated family apparently derived from a stock that became aquatic independently of the near ancestors of any other recent Nematocera.

All known larvae have an unpaired prothoracic proleg (fig. 6) and a very short unpaired proleg on the ninth[2] abdominal segment. Both prolegs are

[2] I agree with Grünberg (1910) that there are at least nine abdominal segments. Puri (1925) considers that there are only eight, but the metameric arrangement of the chief longitudinal muscles clearly shows that there are nine distinct segments with possibly the remains of a tenth more or less completely fused to the ninth. The disposition of the abdominal setae also supports the view that the last apparent segment consists of a partial fusion of the ninth and tenth segments.

armed with numerous rows of fine strongly curved crochets. The method of crawling has been described by Tonnoir (1922), Puri (1925), Hora (1927, 1930), and Grenier (1949). The larvae remain most of the time in an erect position fixed to the substrate by the posterior proleg. When crawling they move in a peculiar looping manner, like the larva of a Geometrid. The head is first brought down and a silken mesh produced by the labial glands is stuck to the substrate. The

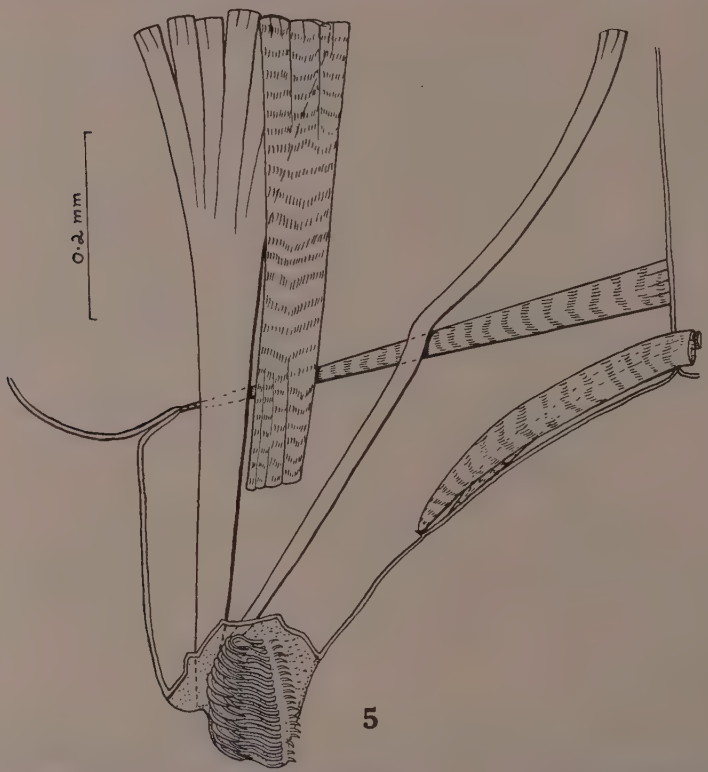


Fig. 5.—*Thaumalea verralli* Edwards, mature larva. The single median proleg of the prothorax as seen from the left side. The proleg retractors are unshaded. The two ventral muscles inserted near the base of the proleg originate in the mesothorax.

crochets of the anterior proleg are then engaged in this mesh. After this is accomplished, the posterior proleg is released and brought forward, by bending the body into a loop, and then engaged in the same mesh. When the posterior proleg is firmly anchored, the anterior proleg is disengaged, and another silken mesh is stuck down a short distance ahead.

Simuliid larvae do not swim. When suitably stimulated, they will release their posterior proleg and float downstream at the end of a silken line that is fairly rapidly pulled out from the opening of the salivary duct by the friction

of the water against the larva. The other end of the silken line is attached to the support they have just quit ; and they are able to crawl up the line against the current. In this process the anterior proleg and crochet-like hooks on the labrum are used. Their method of hauling themselves upstream has been described by Hora (1930 : 216), "The thoracic proleg and the labrum work in opposition to haul up a larva along the silk thread to its former support . . . In the first position the animal is seen to be fixed to the thread by means of the

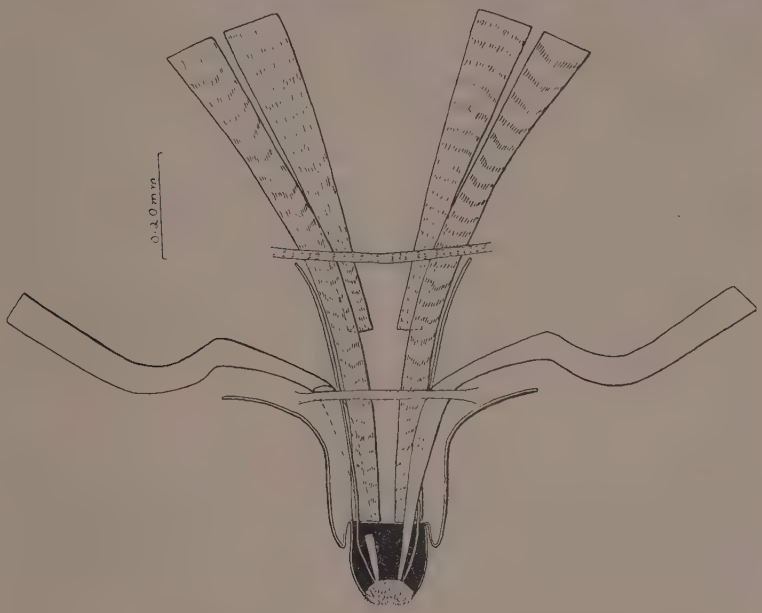


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FIG. 6.—*Simulium latipes* Meig., mature larva. Musculature of the median proleg of the prothorax as seen from above. The muscle inserted at the base of the proleg and that inserted behind the base originate on the posterior margin of the mesothorax. The proleg retractors arise within the prothorax.

hooks on the labrum and on the proleg when these two structures are wide apart. The proleg slides forward and its apex comes to lie close to the labrum . Now the labrum slides forwards and the two structures separate again ; it should be noticed that both the structures remain constantly in touch with the thread, and that a sliding movement of only one of them takes place at a time ". When the larva was kept in a tube full of water so that it was hanging at the end of its thread, Hora observed that its hind end was moved continuously from side to side. If by chance the posterior proleg came in contact with the thread, " the larva adopted the characteristic looping movements for progression along the thread ".

The musculature of the anterior proleg has been figured by Puri (1925) and Rubzov (1940). Both writers have overlooked the pair of fine retractors

arising on the sternite and inserted near the apex of the proleg. This pair of muscles has been found in all three species of *Simulium* that were examined.[3] Puri (*op. cit.* : 320) claims that the apical retractors that arise on the dorsal sides of the prothorax, as well as the basal retractors that arise ventrally on the mesothorax, pass beneath a transverse muscle dorsal to the nerve cord. This so-called muscle is a phragma (see fig. 6). Posterior to this transverse phragma is a transverse muscle. Only the basal retractors of the proleg, however, pass beneath this muscle, and they arise on the hind margin of the mesothorax with the sternal pair that are inserted well behind the basal retractors.

The musculature of the posterior proleg is described by Puri (1925) and Grenier (1945, 1947, 1949). There are several retractor muscles inserted in the disk and periphery of the apex of the proleg. Some of these extend through the ninth segment to arise on the hind margin of the eighth. It is common, particularly in the highly specialised Cyclorrhapha, to find muscles that have lost their metameric arrangement in the sense that two separate longitudinal muscles have become one on losing their attachments to the " intersegmental " membrane or phragma. This condition is found in some of the basal retractors of the prothoracic proleg of the Thaumaleidae and Chironomidae, in some of the retractors of one posterior proleg of the Chironomidae, and in some of the retractors of the ventral prolegs of the Ephydridae. In the natural environment of the Simuliid larva the disc of the proleg does not function as a sucker. Fixation to the substrate is solely by engaging the crochets in a mesh produced by the labial glands, as has been shown by Hora (1927).

(vi) *Blepharoceridae.*

The larvae of all known Blepharoceridae live in fast-flowing streams or in waterfalls though they frequently migrate to quieter water when ready to pupate. They feed on algae. On the mid-ventral region of each of the second to seventh abdominal segments there is a large sucking organ. The structure of this organ has been described by Komárek (1914) and Hora (1930), and their accounts of European and Indian species agree in essential details with the South American species I have examined (fig. 7).

Viewed ventrally, the external parts of the sucker consist of an outer flaccid rim and a large central disk of several kinds of closely packed, fine, sclerotised rods radially arranged. The rods of the row before the " fleshy " rim of the sucker are shorter and thicker than those of the central row and their apices are curved upwards and directed towards the centre. In the centre of the disk is a round hole that is the opening into a large internal chamber, as shown in fig. 7. The outer " fleshy " rim is narrowly incomplete at its median anterior margin, and the gap thus formed functions as a valve to permit the expulsion of the water when the sucker is pressed to the substrate, and probably, as Hofender (1928) suggests, to permit its inflow before detachment. The lateral walls of most of the internal chamber are heavily sclerotised, and this heavily sclerotised part of the chamber is joined to the internal perimeter of the hole in the external disk by a short and more or less membranous tube. The roof of the chamber is closed by a membranous covering. The area of this membranous roof is much greater

[3] Since the section on Simuliidae was written, the muscles of the prothoracic proleg have been correctly described by Grenier (1949).

than is necessary to close the chamber, so that in a relaxed state it is folded as shown in the figure (fig. 7). Three pairs of large muscles that arise on the tergite are inserted in the middle of the membranous roof, and the area around their insertions is much thickened and strongly sclerotised. It is this thickened area of the roof of the chamber that is commonly known as the " piston ", a term that conveys a false impression of its function, since its outer diameter is much less than the inner diameter of the chamber, and, moreover, by its retractor muscles it can be pulled above the top rim of the sclerotised part of the chamber.

After the sucker is pressed against the substrate and most or all of the water beneath it expelled through the anterior valve, the volume of the chamber is chiefly increased by the retractor muscles inserted in its roof. Several muscles,

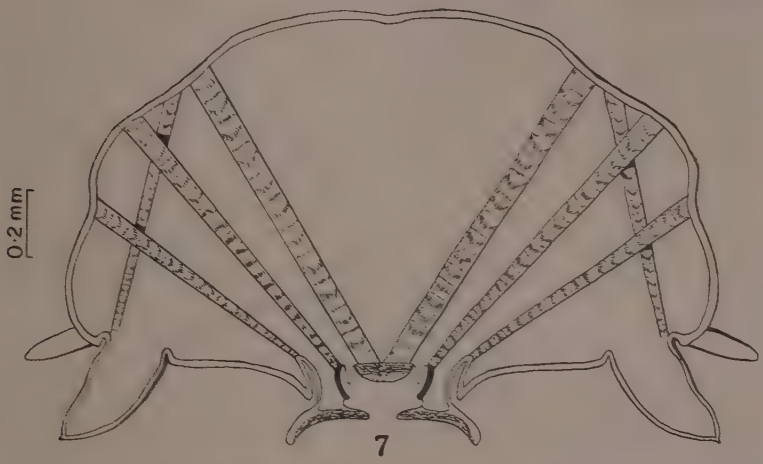

FIG. 7.—Blepharoceridae (*Edwardsinia* sp.) from Chili. Transverse section through sixth abdominal segment of mature larva. For further explanation see text.

also arising on the tergite, are inserted on the rim of the sclerotised wall. A contraction of these also increases the volume of the chamber by straightening the membranous walls that effect its continuity with the internal rim of the hole in the external disk.

Both Tonnoir (1933) and Hora (1933) are agreed that the suckers of the Psychodidae and Blepharoceridae are independently evolved, but Hora attempts to trace those of both groups from a presumed ancestor that had prolegs which became fused. According to Hora (1933 : 285) : " The case of the Dipteran larvae, as well as those of several other insect larvae is different. Some of them possess pseudopods for progression on land, for burrowing or for crawling about in vegetation. When, by competition or some other impelling force, a number of them are obliged to invade flowing waters, these very pseudopods help them in fixation. Under the stress of stronger and stronger currents, the pseudopods become more and more perfected as organs of adhesion till in the Blepharoceridae, that live in the fiercest currents, they assume the form and function of perfect vacuum suckers." This view of the evolution of the ventral suckers is

improbable in so far as it postulates the development of pseudopods in a terrestrial ancestor before its invasion of water. It is nearly always the case that dipterous larvae develop pseudopods only when they become semi-aquatic or aquatic. So far as the Psychodidae are concerned, it is clear enough that their ventral suckers were not evolved from prolegs. It may, however, be believed that the suckers of the Blepharoceridae were evolved from an ancestral aquatic form having ventral paired or unpaired prolegs on the abdomen Since the suckers of all recent Blepharoceridae are very similar in structure, no evidence is available against this view except that by analogy with the Psychodidae it does not appear probable.

Near the lateral margin of the second to seventh abdominal segments of the mature larva there is a stout and more or less cone-shaped, movable appendage. When the sides of the segments are produced laterally, as in most Blepharoceridae, the movable appendage is near the ventral apex of the produced part. Each appendage or proleg is moved by a single muscle inserted near its base (fig. 7). This muscle arises on the tergite. The surface of the appendages is densely setose, and each has a more or less distinct pad near its apex. These pads are sometimes clothed with fine, hooked setae.

According to Hora (1930), the larva maintains its long axis at right angles to the current when crawling, and the appendages on the leeward side prevent it from slipping. Although the larvae may sometimes move at right angles to the current, in those South American species that I have observed the long axis of the body was usually parallel to the current. Tonnoir (1930 : 204) says : " The larvae do not move sideways, as is described by several authors, unless they are disturbed and taken out of the element ; they move straight forwards with a sort of undulating movement, so that when the suckers let go their hold, they are fixed a little forwards, each in turn, but the undulation, which is in no way jerky, starts again anteriorly before the previous one has reached the extremity of the body."

In some genera, e.g. *Edliponeura* Tonn. and *Edwardsinia* Alex., slightly antero-dorsad from the base of each appendage is another smaller, rather similar, non-muscled appendage (fig. 7) of unknown function.

In many genera the form of the lateral abdominal appendages is considerably altered at each moult. In *Paracurupira chiltoni* Campbell, of New Zealand, the first instar larva has retractile, crochet-bearing prolegs on each of the lateral appendages (Tonnoir, 1924). These crochet-bearing retractile parts of the appendages are lost at the first moult, and the form of the appendage in the second and following instars is not very dissimilar from those of other Blepharoceridae. According to Bischoff (1928), the first instar larva of the European *Hapalothrix* (*lugubris* Loew ?) and *Liponeura cinerascens* Loew have retractile prolegs similar to those of *Paracurupira*. *Curupira* is also said to have retractile prolegs in the first instar.

The fate of the apical retractor muscles at the first moult is not known, but both crochets and eversible membrane are lost or much reduced. The sub-apical hook-bearing pad of some Blepharoceridae possibly represents all that is left in the second instar of the retractile portion. The lateral appendages are prolegs that have in the first instar of some, but not all, species a distal crochet-bearing sac on the apex of which are inserted retractor fibres. The prolegs of the first instar of *Edwardsinia* and some other genera have no retractile apical part

(Tonnoir, 1924). From the ontogenetic sequence observed in the structure of the prolegs of some genera it appears possible that the type of prolegs possessed by the mature larvae of all species, and the first instar larvae of some (e.g. *Edwardsinia*), are derived from prolegs with a retractile distal part similar to those of *Paracurupira* and its allies. According to various accounts, the action of the suckers is relatively weaker in the first than in later instars, and this relative weakness may account for the retention of the retractile portion and its muscles in the first instar of some species.

Among recent Diptera, the Blepharoceridae appear to have no close relatives. They are not closely related to the Psychodidae, as has been pointed out by Crampton (1926) and Tonnoir (1933). Adult Blepharoceridae have retained many more primitive characters than have the Psychodidae, e.g. tibial spurs, ocelli, the long anal vein, and the non-twisted hypopygium. That the ventral suckers of the two families are of independent origin is further shown by the fact that the probable evolution of the ventral suckers of the Psychodidae can be traced within that family itself. In the Blepharoceridae, therefore, two very different kinds of abdominal appendages have been evolved to meet two different specific requirements of the relation now established between the larva and its environment.

(vii) *Deuterophlebiidae.*

Only two species have been described, one from the Altai mountains and the other from Japan, but larvae of others are known from western North America. The larvae live in clear, rapid streams on pebbles and rocks exposed to the current. They apparently feed on diatoms and other algae. On each side of each of the first seven abdominal segments there is a long lateral extension, and on the apex of each of these fourteen extensions is a proleg that can be retracted within the extensions by two retractor muscles described by Pulikovsky (1924). The apices of the prolegs bear a large number of crochets, each of which is toothed at its apex.

The Deuterophlebiidae are not closely related to the Blepharoceridae or any other known Nematocera. Their prolegs are independently evolved, and they cannot be considered to have been derived from those of any other recent Nematocera.

(viii) *Psychodidae.*

The larvae are, so far as is known, all phytophagous or saprophagous. There are many aquatic and subaquatic species. None of these have prolegs, but a few have ventral suckers. Most of the aquatic larvae live near the surface in ponds and slow streams, but some live among algae and water plants in the swifter parts of the stream. On the dorsal surface there are usually numerous long and rather stiff, backwardly directed setae. Larvae in streams are generally so oriented that the head is upstream, and, as stated by Miall and Walker (1895: 143), the backwardly directed setae of the dorsal surface, by becoming entangled in the vegetation, prevent the larvae from being swept away by sudden increases in the strength of the current.

In *Sycorax* Haliday and *Horaiella* Tonn. there is a fringe of fine hairs enclosing much of the ventral surface, and the whole of the area thus enclosed functions as

a sucker, according to Feuerborn (1932) and Tonnoir (1933). *Sycorax* lives in damp moss in Java, and *Horaiella* has been found in India in company with young Blepharocerid larvae by a waterfall on stones splashed with spray. *Neotelmatoscopus* Tonn. of India and Java has a single median sucker on segments 2–7 of the abdomen. *N. horai* Tonnoir was found by a waterfall with *Horaiella*. *Maruina californiensis* Kell. has one sucker on each of segments 1–8 as have three Brazilian species of the genus described by Müller (1895). The species described by Müller were found on the sides of a waterfall exposed to the spray. The species found beside waterfalls in torrential streams are almost certainly exposed from time to time to the full force of the current, since one of the most characteristic features of mountain rivers and streams is their considerable rise and fall over very short periods of time.

The evolution of the ventral suckers has been discussed by Hora (1930, 1933) and Tonnoir (1933). Tonnoir believes that the suckers of *Neotelmatoscopus* were evolved from suckers like those of *Sycorax* and *Horaiella*, which have a single sucker that includes much of the area of the ventral surface. According to him, an intermediate stage between *Horaiella* and *Neotelmatoscopus* is probably represented by such recent forms as *Maruina californiensis* Kell. in which, he claims, the hair fringe is regularly interrupted to form a series of oval, more or less complete discs. Tonnoir's theory is diagrammatically shown in fig. 8.

Hora (1933), on the other hand, insists that the ventral suckers are modified prolegs and not new organs like the suckers of fish and tadpoles. He believes that the ancestors of the aquatic Psychodidae were terrestrial forms with prolegs, and that when some Psychodidae became aquatic their prolegs were modified to form suckers. Since in the Diptera prolegs are, with very few exceptions, developed only in an aquatic or subaquatic environment, Hora's theory is most improbable.

Observations on larvae of *Pericoma* Haliday crawling on a damp glass plate show that, even in species without suckers, unspecialised areas of the sternites may form feeble suckers by contraction of the appropriate muscles. A slight differentiation of the peripheral cuticle of such an area would increase the efficiency of the vacuum obtained and result in the formation of a recognisable sucking organ. I am inclined to think that Tonnoir's hypothesis is also incorrect in that the suckers of *Maruina* are independently evolved from those of *Neotelmatoscopus* and those of both genera have never passed through any such stage as that represented by *Sycorax* and *Horaiella*. In this connection it is interesting to note that most, if not all, of the species of *Telmatoscopus*, a genus closely related to *Neotelmatoscopus*,[4] certainly do not have sucking organs.

(ix) *Tipuloidea*.

Until fairly recently the Ptychopteridae and Tanyderidae were usually given subfamily status in the Tipulidae. Alexander (*in* Usinger *et al.*, 1948) and others now accord them family rank, so that in the superfamily Tipuloidea there are now five recognised families: Trichoceridae, Anisopodidae, Tanyderidae, Tipulidae, and Ptychopteridae.

[4] According to Tonnoir (1933), *Neotelmatoscopus* is no more than a subgenus of *Telmatoscopus*.

The Trichoceridae and Anisopodidae live in semi-liquid decaying vegetable and animal matter. *Anisopus* Meig., for instance, is found in cesspits, wet cow-dung, and in sap exuded from tree wounds. Prolegs are absent in all known species. Not only are prolegs absent, but, in the species I have able been to examine of both families, creeping welts are also absent, as they are in *Mycetobia* Meig. and *Olbiogaster* O. S. described by Keilin and Tate (1940).

The Tanyderidae are found in wet decaying wood usually in water. The

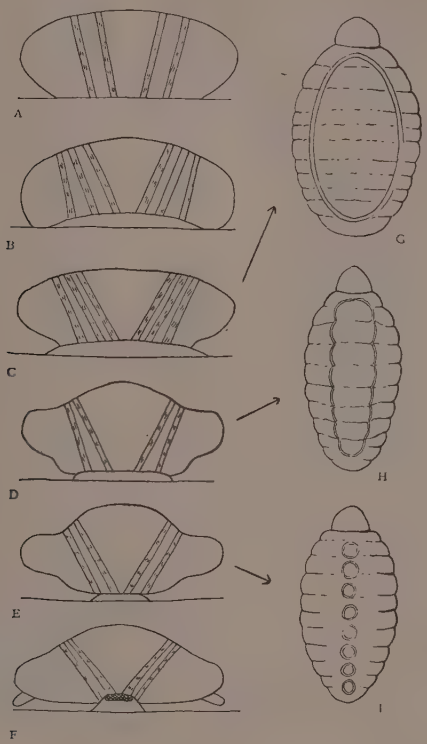

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Fig. 8.—Tonnoir's theory of the evolution of ventral suckers in Psychodidae and Blepharoceridae. (A) First stage of adaptation to rapid streams : larva dorso-ventrally flattened with a large surface of adhesion ; (B) stage in which there is a sucker action of the whole ventral surface brought about by the action of the dorso-ventral muscles ; (C) a pleural fringe of hairs or a pleural membrane is evolved to facilitate the retention of the vacuum, as in *Sycorax* Hal. and *Horaiella* Tonn.; (D) stage in which the pleural fringe or membrane is nearer the median line and the mobility of the larva is greater ; at this stage the fringe may be continuous, as in *Horaiella* Tonn., or it may be interrupted to form a series of oval more or less complete discs, as in *Maruina californiensis* Kellog ; (E) stage of *Neotelmatoscopus* Tonn.; (F) stage evolved when the larva invades swifter currents and a sucker of the Blepharocerid type is formed ; (G), (H) and (I) are the stages corresponding respectively to sections (C), (D) and (E) as seen from below (after Tonnoir, 1933).

only species I have been able to examine is *Protoplasa fitchii* O. S., and this has two long and slender, crochet-bearing anal prolegs.

The larvae of a large number of Tipulidae are semi-aquatic or aquatic, but probably most species live in damp earth and in moist rotting wood. Most are metapneustic, but a few aquatic species are apneustic. Well developed retractile prolegs are present in only some of the species that normally live beneath the surface of the water. Among the latter, the only species known to me that have prolegs are species of Limoniinae-Pediciini. Of the species which I have bred, *Pedicia rivosa* L. and *Crunobia littoralis* Meig. have a pair of prolegs on each of segments 4–7, whereas *Tricyphona claripennis* Edw. has paired prolegs on segments 3–7. The prolegs of *Pedicia* and *Crunobia* are setose but lack crochets, whereas those of *T. claripennis* are armed as shown in fig. 9.[5] In the latter species each proleg has an incomplete apical circle of about 35 crochets (4th instar). Slightly proximal to this is another incomplete circle consisting of many more crochets that are only about half as long. In *Dicranota bimaculata* Schumm. (Miall, 1893, 1895) the number and form of the prolegs is as in *T. claripennis*, but there are three rows of crochets according to Miall. From the account given by Alexander (1920) it would appear that the prolegs of *Pedicia albovitta* Walker are like those of *P. rivosa*, whereas the prolegs of *Rhaphidolabis tenuipes* O. S. are like those of *T. claripennis*. The aquatic larva of *Trimicra pilipes* Meig. has a pair of crochet-bearing prolegs on each of abdominal segments 3–7 (Grünberg, 1910). Malloch (1917) includes this species in the Pediciini.

The proleg muscles of *Tricyphona claripennis* Edwards are shown in fig. 9. The musculature of the prolegs of *Pedicia rivosa* L. (fig. 10) is similar to that of the prolegs of *T. claripennis*. The first three pairs of prolegs are muscled like each other, but each proleg of the seventh segment has an additional muscle that is larger than the other proleg muscles and that, unlike them, extends obliquely above instead of under the first main longitudinal muscle of the sternite.

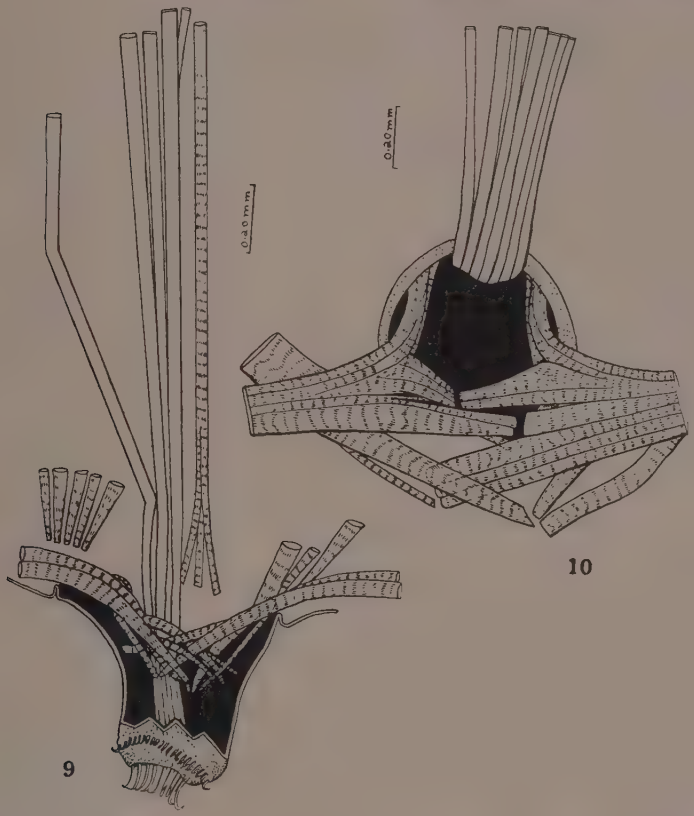
The only terrestrial species of Pediciini that have been bred by me, *Tricyphona immaculata* Meig. and *T. schummeli* Edw., lack prolegs.[6] These species have slightly transverse, median, ventral, creeping welts on abdominal segments 4–7. These well-muscled and somewhat retractile welts are intermediate in form between creeping welts and the usual kind of prolegs; they illustrate clearly the difficulty of drawing a hard and fast line between the two kinds of structures. According to Malloch (1917), the larva of *Epiphragma fuscipennis* Say, that lives in decaying stems in the mud at the edge of shallow pools, has a single ventral proleg on segments 2–7 of the abdomen. I suspect, however, that these structures are creeping welts. I have bred *Epiphragma ocellaris* L., and this species has only creeping welts, as has the allied *Austrolimnophila ochracea* Meig.

A number of species in different groups of the Tipulidae live beneath the surface of the water but have no prolegs and yet are as aquatic as any of the species that have. Among these are species of Cylindrotominae and Limoniinae. The mode of life of these differs greatly: Cylindrotominae, such as *Phalacrocera*

[5] Hennig (1950 : 432) has figured the prolegs of *Pedicia* and *Dicranota*. His fig. 235 is of *Dicranota* and not of *Pedicia*, whereas his fig. 236 is of *Pedicia* and not of *Dicranota*.

[6] The type of the genus *Tricyphona* is *T. immaculata* Meig. A new genus is required for the aquatic *T. claripennis* Edw., which has a very different larva and pupa.

Schiner, are densely clothed with long tracheal gills and live curled about or entangled in submerged mosses. Some genera of Cylindrotominae have numerous ventral processes, but these have no intrinsic muscles, and I have, somewhat arbitrarily, not considered them as prolegs. Many of the aquatic Eriopterini and Hexatomini live in more or less liquid organic mud beneath the surface of the water, and, as might be expected, do not have prolegs. Other Hexatomini,



FIGS. 9, 10.—(9) Inner view of right proleg of sixth abdominal segment of fourth instar larva of *Tricyphona claripennis* Edwards. (10) Inner view from above of right proleg of fourth abdominal segment of fourth instar larva of *Pedicia rivosa* L.

e.g. *Limnophila* (*Elaeophila*) *verralli* Berg. and *L.* (*E.*) *apicata* Loew, both of which I have bred in large numbers, live in sand at the edges of streams. The absence of prolegs in such species of *Limnophila* is more difficult to account for, particularly as they are found in the same kind of environment as some of the Pediciini with prolegs. A number of Limoniini are aquatic, e.g. the apneustic genus *Taphrophila* Rondani, the intertidal species of *Geranomyia* Hal., and I have recently found *Dicranomyia mitis* Meig. in algae in the swift parts of streams.

All of these, especially *Taphrophila*, have well-developed ventral abdominal creeping-welts, but, so far as I am aware, no species in the tribe Limoniini has prolegs.

The Ptychopteridae are usually found in decaying vegetable debris that is either floating or on the surface or slightly beneath the surface. They are phytophagous. The caudal breathing tube bearing the spiracles at its apex is usually very long and partly or entirely retractile. The larva usually remains sufficiently near the surface to be able to reach through the surface film with its breathing tube. The larvae of *Bittacomorpha* Westw., *Bittacomorphella* Alexander and *Ptychoptera* Meig. have been described (Malloch, 1917 ; Johannsen, 1934 ; Alexander *in* Usinger *et al.*, 1948). Each genus has a pair of ventral retractile prolegs on each of the first three abdominal segments, and every one of these prolegs has a single long curved crochet at its apex. The only Ptychopterids I have examined are British species of *Ptychoptera*. These have, in addition to the three pairs of ventral prolegs, a lateral proleg on each side of segments 1–5. The lateral prolegs have no distinct crochets, but are densely and finely setose. The creeping-welts, in which many muscles are inserted, are somewhat irregularly swollen so that it might be claimed that some of these swellings are prolegs, the distinction between swellings of the welts and well-developed prolegs being only one of degree. For instance, slightly ventral from each lateral proleg there is a distinctly circumscribed swelling in the creeping welt that might be counted as a proleg.

So far as is known, the larvae of all of the Ptychopteridae are aquatic. *Ptychoptera*, and probably also the other genera, will survive and pupate if the water dries up, providing the debris in which they are living remains damp.

Among the Tipuloidea, then, prolegs are developed only in subaquatic and aquatic species but by no means in all species with such habits, and they are found in their most developed form amongst those species that are truly aquatic. Within the super-family the independent development of retractile prolegs may be discerned in at least three groups : Tanyderidae, Pediciini (Tipulidae), and Ptychopteridae.

Of some interest also is the evolution within the superfamily of smooth, elongate forms with an eel-like method of locomotion in such environments as semi-liquid decomposing vegetable or animal matter—environments in which similar forms are produced in other families, for instance, the Ceratopogonidae.

(x) *Rhagionidae* (= *Leptidae*).

Most Rhagionidae are predaceous and live in decaying wood or in the ground. Only two genera are known to be aquatic, *Atherix* Meig. and *Symphoromyia* Frauenfeld. The terrestrial species have creeping welts that are especially well developed in the Xylophaginae living in decaying wood and under loose bark. The species of *Atherix* live in streams, and all have a pair of very well developed ventral prolegs bearing crochets on each of the first eight abdominal segments. In *A. variegata* Walk. (Johannsen 1935) and some others, each proleg of segments 2–7 is nearly divided to form two. Some species of *Symphoromyia* are said to be aquatic, but I have not seen the larvae of any of these. The terrestrial species of *Symphoromyia* lack prolegs.

The balance of evidence suggests that the Rhagionidae are a terrestrial

group and that *Atherix* and some species of *Symphoromyia* have invaded the water independently of each other, *Atherix* at least evolving prolegs as a result of its aquatic existence. The Rhagionidae are all or nearly all amphipneustic except for the species of *Atherix*, which are apneustic.

The worm-lions of the subfamily Vermileoninae (*Vermileo*, *Lampromyia*, *Vermitigris*) live in dry places where they excavate little funnel-like pits in the dust or sand. They feed upon ants and other small insects that fall into their pits. The worm-lions throw grains of sand or particles of dust at insects attempting to crawl up the sides of their pits. In so doing they cause miniature landslides that often bring the escaping insect to the bottom of the pit within reach of their jaws. All of the known species have a single proleg on the mid-ventral surface of the first abdominal segment. The proleg has a number of stout apical setae. Shelford (1900) and others point out that the prey is grasped between the proleg and the thorax in such a way that the proleg is being used as a thumb. Engel (1929) claims that the pseudopod is grasped by the mouth-parts and that when the appropriate muscles are contracted its sudden release throws the thorax and head violently back. He says that in this way the sand and remains of dead insects are tossed out of the pit. Wheeler (1931) disputes this account and says that the function of the pseudopods is to wipe off with their stiff spines particles that adhere to the mouth-parts. My own observations on *Vermileo*, made long ago, were too superficial to contribute to this problem, but it is certain that at times the proleg is used to hold the prey. The proleg can hardly be used to anchor the larva since its normal position in the sand is with its ventral surface uppermost. In considering Engel's observations, it should be remembered that various groups of dipterous larvae have developed methods of leaping that involve grasping projections of the body with their mandibles (see p. 460). When the worm-lions are exposed, however, they do not leap in this way, as shown by Wheeler (1931).

There is no evidence whatever for believing that the single proleg of the Vermileoninae is an organ preserved from a former aquatic ancestor. The evidence is strong that it was evolved during the process of adaptation of the ancestral Vermileonid to its peculiar mode of existence in sand and dust. Wheeler (1931, p. 178) supposes that all dipterous larvae are derived from forms with paired prolegs, an opinion he could hardly have held had he been familiar with a wider range of larvae. The Vermileoninae are thus a clear exception to my generalisation that dipterous larvae evolve prolegs usually only during an aquatic existence ; and they are not the kind of exception that proves the rule.

(xi) *Tabanidae.*

Most Tabanid larvae are aquatic or subaquatic, living either below or above water level in the wet sand or mud of the banks of streams and ponds. A number of species, however, normally live in earth or rotten wood some distance from water. But even these species are always found in relatively damp places, and no species is known to prefer relatively dry soil. The egg-masses of most species are laid on stems or leaves above streams and ponds, and this is true even of many of those species the larvae of which live above water level in the sand or mud of the banks. The eggs of the latter are so laid that the larvae fall into the water on hatching and must subsequently make their way to the bank.

Apparently only one species, *Tabanus stigma* Fab., is found on the seashore, all other aquatic or subaquatic larvae being freshwater forms. All Tabanid larvae are predaceous, feeding mainly on insect larvae, crustacea, and oligochaetes and all are metapneustic.[7]

The available evidence suggests that the recent Tabanidae are derived from an aquatic or subaquatic group: (1) the larvae are all metapneustic, and the spiracles of the eighth abdominal segment are apical and very close together; (2) the great majority of the known species are aquatic or subaquatic; and (3) the females of nearly all species oviposit over water, and this habit is retained even in many of those species the larvae of which leave the water after hatching and develop on land.

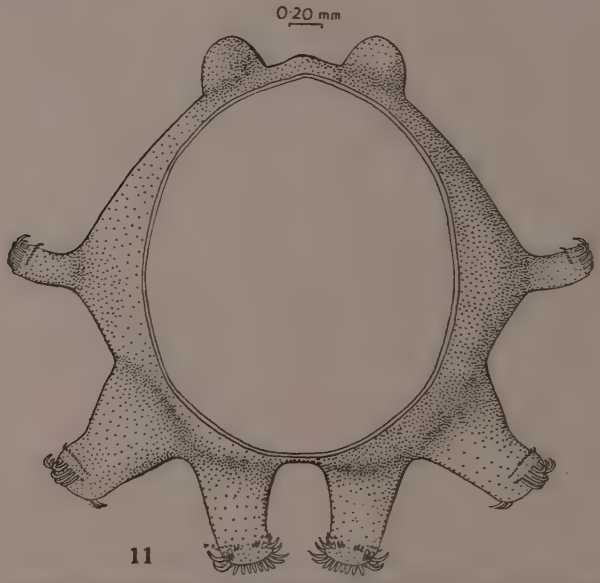


FIG. 11.—*Tabanus kingi* Aust. Prolegs of third abdominal segment of mature larva.

Amongst recent species two main evolutionary trends may be distinguished. Firstly, there is a further adaptation to a completely aquatic existence during which process certain conspicuous respiratory adaptations are evolved, for instance: (1) the eighth abdominal segment becomes modified to form a syphon capable of being telescoped and extended; (2) the longitudinal tracheal trunks become dilated and function as air-sacs, as in many species of *Tabanus*; and (3) the spiracles of the eighth abdominal segment of some species of *Chrysops* (*C. celes* O. S. and others) become modified for tapping the intercellular air-spaces of roots and stems (Hinton, 1953). Secondly, there is a further adaptation for a strictly terrestrial existence evidenced by a reduction of the prolegs in some species that are already definitely terrestrial, e.g. *Haematopota pluvialis*

[7] I have not seen the larva of *Haematopota* Meigen, which some writers claim is amphipneustic.

L. and *Goniops chrysocoma* O. S. Species that are terrestrial tend to have, as pointed out long ago by Brauer, an eighth abdominal segent that is capable of being alternately extended and telescoped.

There is nothing to suggest that the ventral series of prolegs of the Tabanidae do not represent a further instance of the independent evolution of prolegs. However this may be, the dorsal and lateral prolegs are clearly of independent origin. Not only are they of independent origin so far as the family is concerned, but there is evidence that some of the prolegs have been independently evolved several times even within the same genus. For instance, the single ventral proleg of the eighth segment of *Tabanus kingi* Austen is clearly evolved from a preanal creeping welt like that of other species. The presence of a dorsal pair of prolegs on several or all of the first seven abdominal segments (Table I) in unrelated species of *Tabanus* from different regions of the world seems to be good evidence that these pairs were evolved independently several times within the genus.

The evolution of prolegs from creeping welts is shown more clearly in the Tabanidae than in any other group of endopterygote larvae. For instance, the dorsal prolegs simply represent a local enlargement and specialisation of the dorsal part of the transverse creeping welt. So far as external form and musculature are concerned, all intermediate conditions can be found between a simple dorsal welt and one modified to form well-developed prolegs (figs. 11–15). When the dorsal creeping welt is slightly swollen on either side of the median line, it becomes merely a matter of opinion as to whether these swellings are to be called prolegs or not, and it is these intermediate structures that have given rise to many of the discrepancies in the literature as to the number of prolegs possessed by certain species of *Tabanus*.

Within the genus *Tabanus* it has not been possible to establish a definite correlation between the specific conditions of life and the number of prolegs. The number of species that I have been able to examine is too few and published accounts are too unreliable for this. For the same reason I have been unable to find a correlation between the presence of crochets on the prolegs and a particular kind of environment. Nevertheless, it may be noted that one of the few species with 42 instead of 54–57 prolegs is the terrestrial *T. sulcifrons* Macq. (Davies, 1919). *Tabanus kingi* Austen, which is unusual in living under stones in the swift parts of streams, is the only known Tabanid with a well-developed anal proleg. The females of *T. kingi* have the apparently unique habit (in Tabanidae) of laying their egg-masses on stones exposed in streams instead of on overhanging, leaves or stems, as is usual (King, 1910).

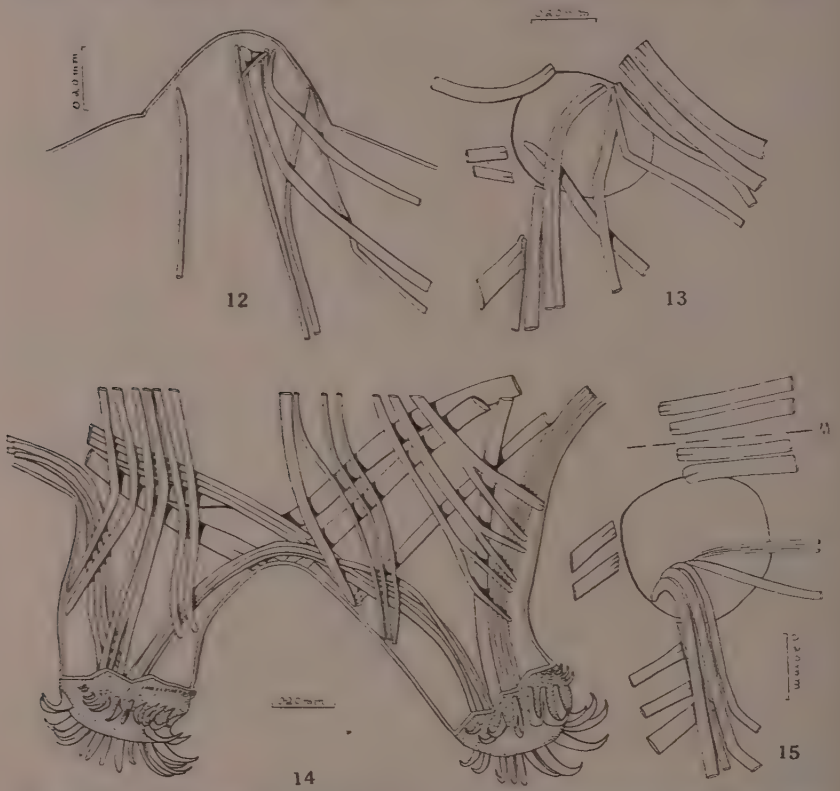
Some of the species of *Tabanus* have large crochets on all eight prolegs of the first seven abdominal segments, in many others some of the anterior dorsal prolegs lack crochets, e.g. in *T. kingi* Aust., whereas in some, e.g. *T. pertinens* Aust., none of the prolegs are armed with more than moderately fine setae.

In addition to the papers already mentioned, this account of the Tabanidae is also based on the papers of Marchand (1920) and Stone (1930).

(xii) *Asilidae.*

All known Asilid larvae are predaceous and amphipneustic. Malloch (1917) and Melin (1923) have mistaken the external scars of the non-functional spiracles

for functional spiracles, but in the Asilidae, as in other Brachycera-Orthorrhapha, there are not more than two pairs of functional spiracles. The abdomen is 9-segmented, as stated by Malloch (1917) and many earlier writers. Melin (1923 : 120) believes the abdomen has only eight segments because there are



FIGS. 12–15.—*Tabanus kingi* Aust., mature larva. (12) Right dorsal proleg of third abdominal segment. (13) Inner view from below of the right dorsal proleg of the fourth abdominal segment. (14) Ventral (left) and subventral (right) prolegs of the third abdominal segment. (15) Inner view from below of left dorsal proleg of seventh abdominal segment ; (*M*) median dorsal line.

only eight discrete abdominal ganglia, but the eighth ganglion is evidently compound. Other endopterygote larvae that clearly have ten segments have only eight discrete ganglia, the eighth " ganglion " consisting of at least three fused ganglia.[8]

[8] Most endopterygote larvae have fewer than eleven distinct abdominal segments. So long as the primitive segmentation is preserved in the embryonic mesoderm, it is evident that if the apical " segment " is not the eleventh it must consist of a fusion of two or more segments. For instance, if the apical is the eighth, it must consist of the fused eighth, ninth, tenth, and eleventh segments, just as the absence of segmental lines in the cranium

The Asilid larvae that I have examined, and all those that have been adequately described, have at least some pairs of ventral prolegs. The distribution of prolegs in some typical forms is shown in Table II. Dissection of the prolegs of *Laphyria* shows that all have apical retractor muscles. The Dasypogoninae and Asilinae live in the ground, usually in sandy soils, and the Laphyrinae live in the wood or beneath the bark of dead trees.

The presence of prolegs suggests that the Asilidae have had an aquatic ancestor because it can be shown that nearly every other dipterous larva with prolegs is aquatic or has had an aquatic ancestor. At the same time it must be especially stressed that in claiming that prolegs develop as a rule only in subaquatic forms, the Asilids must be considered to be an important exception to the rule so long as no independent evidence for an aquatic ancestral Asilid is available.

The species of *Laphyria* have a transverse row of six or eight prolegs on each of the first six abdominal segments, and it is perhaps significant that although they are often found boring in decaying tree stumps they are also often found in liquid or semi-liquid matter between the bark and the wood that has not been liquified. The Asilinae and Dasypogoninae that live in the ground have, on the other hand, not more than one pair of prolegs on each segment.

TABLE II.—*The distribution of prolegs in some species of Asilidae. Most records from Melin*, 1923.

Species.	Segments.										Total.
	I	II	III	1	2	3	4	5	6	7	8	9	
Asilinae :													
Epitriptus cingulatus F.				2	2	2	2	2	2	.	.	.	12
Philonicus albiceps Meig.				2	2	2	2	2	.	.	.	.	10
Pamponerus sp.				2	2	2	2	2	2	.	.	.	12
Dasypogoninae :													
Leptogaster cylindrica Deg.				.	2	2	2	2	2	2	.	.	12
Dioctria hyalipennis F.				2	2	2	2	2	2	.	.	.	12
Lasiopogon cinctus F.				2	2	2	2	2	.	.	.	.	10
Cryptopogon lateralis F.				2	2	2	2	2	2	2	.	.	14
Laphyriinae :													
Laphyria gilva L.				8	8	8	8	8	8	.	.	.	48
flava L.				6	6	6	6	6	6	.	.	.	36
sp.				6	6	8	8	8	8	.	.	.	44
sp.				6	8	8	8	8	8	.	.	.	46

(xiii) *Mydaidae, Bombyliidae and Nemestrinidae.*

The Mydaidae, Bombyliidae, and Apioceridae are included by Malloch (1917) with the Asilidae in the superfamily Asiloidea. The larvae of the Mydaidae and Bombyliidae are similar to those of the Asilidae in having a 9-segmented abdomen and an amphipneustic respiratory system in the mature larva. They are carnivorous like the Asilidae. The larva of *Mydas clavatus* Drury is found in decaying wood, where it feeds on beetle larvae. According to Malloch (1917 :

does not alter the fact that the cranium is the product of a fusion of several segments. For this reason, when one speaks of an 8-segmented larval abdomen, the first seven segments correspond to metameres, but the eighth " segment " consists of several metameres that become fused during ontogeny and that often separate again in the pupa and imago.

371) each of the middle ventral segments of the abdomen has a " transverse series of 4 rather irregular pseudopod-like elevations near anterior margin ".

On available evidence it is not possible to determine with any degree of certainty if the prolegs of the Mydaidae are independently evolved from those of the Asilidae or if the ancestral form from which the Asiloidea arose possessed prolegs that have been lost in varying degree in different groups within the Asiloidea.

The larvae of the Bombyliidae are predators and parasitoids of the larvae of the Hymenoptera, Lepidoptera, Diptera, and Coleoptera, and some feed on the egg-masses of grasshoppers. The first instar larvae, e.g. *Hyperalonia* Rondani and *Bombylius* L., have proleg-like ventro-lateral welts on the abdomen. At the first moult these are lost, and the larva becomes amphipneustic instead of metapneustic.

The larvae of the Nemestrinidae resemble those of the Asiloidea in having a 9-segmented abdomen. They are internal parasitoids of other insects, and the mature larva is said to be metapneustic. The first instar larva of some, e.g. *Hirmoneura*, have ventral locomotory proleg-like projections on segments 2–9 of the abdomen (Handlirsch, 1883). These prolegs (?) are lost at the first moult.

(xiv) *Empididae.*

Little is known of the early stages of this family. The larvae are predators or scavengers, living in earth or in rotten wood, and their locomotory organs are creeping-welts, as in *Rhamphomyia dimidiata* Loew, *Drapetis nigra* Meig. (Malloch, 1917), *Empis* L., *Hilara* Meig., *Microphorus* Macq. (Lundbeck, 1910), *Ocydromia glabricula* Fall. (Beling, 1882), and *Platypalpus major* Zett. (Beling, 1888). The terrestrial species have an amphipneustic respiratory system. A few truly aquatic species are known, all in the subfamilies Hemerodrominae and Clinoceratinae. Two Hemerodromiinae have been bred by me : *Chelifera praecatoria* Fall. (also bred by Brocher, 1909) and *Hemerodromia unilineata* Zett. Both are apneustic and have paired, ventral, crochet-bearing prolegs on abdominal segments 2–7. They are commonly found in moss in the swift parts of streams, as are two Clinoceratinae, *Wiedemannia bistigma* Curtis and *Clinocera bipunctata* Hal. also bred by me. Notes on their biology are given by Hinton (1950). They have paired, ventral, crochet-bearing prolegs on the first eight abdominal segments as in the aquatic *Roederiodes juncta* Coq. (Johannsen, 1935) and the aquatic or amphibious *Clinocera barbatula* Mik (Wesenberg-Lund, 1943).

Although only a few Empidid larvae are known, it is significant that of these all the terrestrial species lack prolegs, whereas only the aquatic species have well-developed prolegs. The prolegs are independently evolved at least once within the family, and, owing to the fact that they are present in the aquatic members of both the Hemerodromiinae and Clinoceratinae, it seems possible that within the Empididae prolegs have been independently evolved on at least two occasions.

(xv) *Dolichopodidae.*

The larvae of most species are found in damp earth, in rotten wood, and in humus, and most are predaceous. According to Grünberg (1910), none live in

water. Malloch (1917 : 404), on the other hand, claims that the great majority are aquatic. It now seems certain that very few live beneath the surface so that they are in direct contact with the water. Certainly most of those that live below the surface of the water in leaves and stems (e.g. *Thrypticus smaragdinus* Gerst. in stalks of *Phragmites*) of aquatic plants are not in contact with the water, and their conditions of life are probably not essentially different from those living in plants above the surface of the water. A number of Dolichopodidae are intertidal, and these are regularly immersed, often to considerable depths, at high tide. It is not known if they are active at these times and it is possible that they do not move about but remain still when the tide is in, as do the intertidal Tipulidae. Two intertidal species, common in the Seven Estuary, have been bred by me : *Aphrosylus mitis* Verrall and a species of *Hydrophorus*, probably *H. oceanus* Macq. Neither of these has prolegs, but the creeping welts of both species are well developed on the first seven abdominal segments. The later instars of both terrestrial and intertidal larvae are amphipneustic. It has been claimed that the later instars of *Argyra* are metapneustic (Marchand, 1918), but this is unlikely. Mr. C. E. Dyte has bred *Argyra confinis* Zett. and this species is metapneustic in its final instar. *Thrypticus* Gerst. is said to be peripneustic (Lübben, 1908 ; Johannson and Crosby, 1913), a claim that still requires confirmation since the mature larvae of no other Brachycera-Orthorrhapha have more than two pairs of functional spiracles.

The larvae of various species of *Dolichopus* are said to have prolegs on the first seven abdominal segments (Brauer, 1883 ; Lundbeck, 1912), but those I have bred, and seven British species bred by Mr. C. E. Dyte, have only creeping welts. For this reason we may dismiss earlier claims that the terrestrial species of the genus possess prolegs. A pair of latero-ventral prolegs is present on the eighth abdominal segment of the first instar larva of aquatic species of the Hawaiian species of *Eurynogaster* (Williams, 1939). *Eurynogaster* larvae are found in moss in the swift parts of streams. The prolegs are lost in later instars. The final instar larva of *Systenus adpropinquans* Loew, which has recently been bred by Mr. C. E. Dyte, has a pair of conspicuous prolegs on the first abdominal segment. This larva sometimes lives in the oozing sap of injured trees.

(xvi) *Syrphidae.*

The larvae of many Syrphids have been described. This account is based on an examination of a fair number of species of the chief subfamilies as well as on published summaries, especially that of Lundbeck (1916). A few larvae are phytophagous, but the great majority are either predaceous or saprophagous. These two main groups based on feeding habits also differ both in structure and in the environment they occupy. In the structure of their pharynx they conform to Keilin's generalisation (1917) based on Muscid larvae ; the predaceous species have a simple pharynx, whereas in the saprophagous species the internal surface of the pharynx has finely setose longitudinal ridges. In most of the saprophagous species that I have examined two straining plates and a tituratingorgan are present, similar to those of *Eristalis* L. described by Wilkinson (1901).

In-so-far as habitat is concerned the predaceous species, chiefly Syrphinae, are found, with few exceptions, creeping about the stems and leaves of plants, where they feed primarily on Aphids and scale insects. The saprophagous

species, on the other hand, never normally live on exposed surfaces, but are found in decaying vegetable and animal matter that is often in a semi-liquid or liquid state, in stagnant and putrid pools, and in exudations from tree wounds.

The mature larva of nearly all Syrphids is amphipneustic. In the predaceous species the spiracles of the eighth abdominal segment are sessile or may open on a short cylindrical tubercle, but the eighth segment is itself never modified to form a breathing tube. The saprophagous species belong to two groups, according to whether the eighth abdominal segment is or is not modified to form a protractile breathing tube.

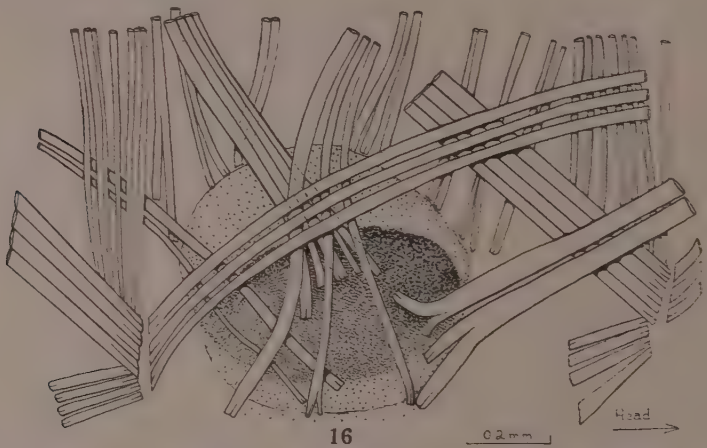


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FIG. 16.—*Callicera rufa* Schummel, mature larva. Inner view from above of the proleg of the third abdominal segment. The musculature of the prothoracic prolegs is similar but not identical.

The variation in the length of the breathing tube of the saprophagous species is great. In some species, e.g. *Callicera rufa* Schumm., it is only a fraction as long as the body, whereas in others, e.g. many Eristalinae, it is many times as long as the body. A breathing tube is clearly an adaptive modification of survival value only in an aquatic environment or one in which the larva is often or always submerged in liquid or semi-liquid substances, such as decomposing vegetable and animal matter. Many of the species with a well-developed breathing tube have been found only a few times, and then in damp rather than liquid vegetable matter, but the possession of a breathing tube would appear to be good evidence that the species normally passes part of its life submerged in a liquid, or at any rate that its recent ancestors did so, and, if the larva now no longer lives sufficiently frequently in such an environment, its breathing tube may be supposed to be in the process of reduction owing to a lack of selective value.

If, then, the possession of a breathing tube is evidence of a life normally spent in water or other liquids, it is interesting to note that every species I have examined that has a breathing tube, whether long or short, also has a pair of crochet-bearing, retractile prolegs on the ventral surface of the prothorax and each of the first six abdominal segments. This is true also of many species known

to me only from description. In the brief descriptions of many other species with a breathing tube no mention is made of prolegs, but this cannot be taken as evidence that these structures are absent.

In previous sections I have dwelt on the fact that dipterous larvae living in tree exudations or in other liquid or semi-liquid vegetable or animal matter tend to loose their prolegs and often become eel-like. No comparable changes in form are undergone by Syrphid larvae living in these environments ; and it therefore appears at first sight that my generalisation concerning the effect on prolegs of liquids more viscous than water is false. But looking at the matter a little more closely, it is evident that the behaviour of Syrphid larvae in such liquids is different from that of other dipterous larvae in certain important respects, as shown below.

Syrphid larvae remain on the bottom, a habit possible to them only because they have a breathing tube, since the oxygen tension in decomposing liquid matter is probably usually too low to support life at the bottom by cutaneous respiration. On the bottom they have a relatively firm substrate that enables the prolegs to function. Smaller dipterous larvae remain much of the time suspended in the liquid, and whether they are apneustic or have one or two pairs of functional spiracles, they must frequently swim to or near to the surface in order to respire. In their movements through the liquid or semi-liquid they can find no firm purchase for prolegs, which thus fail to develop, or, if present when a liquid more viscous than water is invaded, cease to be functional and are in time lost. To this argument the objection might be advanced that, when newly hatched, Syrphid larvae are as small as many others that loose prolegs or fail to develop them. But Syrphid larvae are small for only a relatively short period of their lives and even then usually confine themselves to depths from which their breathing tube can reach the surface.

The importance of body size as a factor in the type of locomotion developed is particularly evident in such environments as tree exudations and the semi-liquid matter beneath the bark of dead trees. Both of these environments are usually so shallow that the eel-like kind of swimming movements used by small larvae, such as those of many Ceratopogonidae, would not appear to be advantageous for Syrphid larvae that are hardly covered by the liquid from the time they are partly grown.

Among the saprophagous forms that have the eighth abdominal segment modified to form a breathing tube and have ventral crochet-bearing prolegs on the prothorax and first six (rarely seven) abdominal segments are many Eristalinae, Milesiinae, Sericomyinae, Chilosiinae, and Cerioidinae, e.g. *Helophilus* F., *Myiatropa* Rond., *Mallota* Meig., *Eristalis* Latr., *Myiolepta* Newm., *Xylota* Meig., *Pocota* Lep. & Serv., *Syritta* Lep. & Serv., *Temnostoma* St Far. & Serv., *Tropida* Meig., *Arctophila* Schiner, *Sericomyia* Meig., *Callicera* Panz., and *Cerioides* Rond. The genus *Neoascia* Will. has been placed in the Syrphinae by Lundbeck (1916), but it lacks the oral structure of predaceous larvae and, moreover, has the eighth abdominal segment modified to form a breathing tube. It has a ventral pair of crochet-bearing prolegs on the first six abdominal segments. The two species known to Lundbeck were found in flood refuse.

So far as I know, only a relatively small number of the saprophagous species lack a breathing tube. These species usually also lack prolegs, but a striking exception is *Volucella* Geoff. Some, if not all, of the species of *Volucella* have

well-developed ventral prolegs with crochets. The species of this genus are scavengers in the nests of wasps and bees. *Volucella* may be derived from a group that lived in liquids, but until this is clearly shown to be the case, it must be regarded as an exception to the rule that prolegs are not acquired in terrestrial dipterous larvae.

The carnivorous species that live on stems and leaves of plants lack prolegs. According to Bhatia (1939) they moisten the surface over which they move with saliva. The same writer points out that on each abdominal segment of *Metasyrphus luniger* Meig. there are six slight swellings in a transverse row, and that similar swellings are present in a few other carnivorous species, e.g. *Sphaerophoria flavicauda* Zett. These swellings are correctly called locomotory swellings by him. But they are very slight swellings without crochets or stiff setae and are not quite comparable to the projections here and by others called prolegs, although the difference is perhaps only one of degree, just as the distinction between a creeping welt and a proleg is not absolute, and intermediate structures are found difficult definitely to assign to one or the other category.

The Syrphinae are not closely related to any other recent family, and their larval prolegs may therefore be said to have been independently evolved from those of any other family. The occurrence of a larva with prolegs and a breathing tube in several different subfamilies suggests either a common origin for these subfamilies or a number of relatively independent evolutionary lines that converge so far as prolegs, a breathing tube, and feeding habits are concerned. In short, opinion as to the number of times crochet-bearing prolegs have been evolved in the Syrphidae must wait upon a more careful study of the phylogeny of the family than has yet been made.

(xvii) *Ephydridae.*

Most of the larvae of this large family are aquatic or semi-aquatic and are either phytophagous or saprophagous. They are amphipneustic or metapneustic, and in some, e.g. species of *Notophila* Fall., *Hydropota* Rond. (= *Hydrella*), and *Lemnaphila* Gray, the spiracles of the eighth abdominal segment open on sharp spines that can be thrust into roots and stems, and thus tap the intercellular air-spaces. The species are usually found in fresh water, but some live in lakes of a salinity higher than that of the sea. A few are found in hot springs and species of *Scatella* R.-D. have been found in springs up to 55° C. One species, *Psilopa petrolii* Coq., lives in pools of crude petroleum in California.

The numerous species of the genus *Ephydra* Fall. live in the water creeping about on submerged plants. On each of the first eight abdominal segments they have a pair of well-developed, crochet-bearing prolegs with apical retractor muscles (figs. 17–18). The sixth and eighth pairs of larval prolegs also function in the pupal and pharate adult stages to secure the puparium to roots and stems as shown in fig. 20. Some of the Hawaiian species of *Scutella* R.-D. have paired prolegs, and these structures are best developed in the most aquatic species (Williams, 1938).

The aquatic larvae of *Notophila* and most other genera do not have prolegs. Although submerged these larvae do not live freely in the water, but are either feeding within decaying roots or stems or are living in the organic ooze on the bottom. Larvae living in the organic ooze of the bottom of ponds and ditches

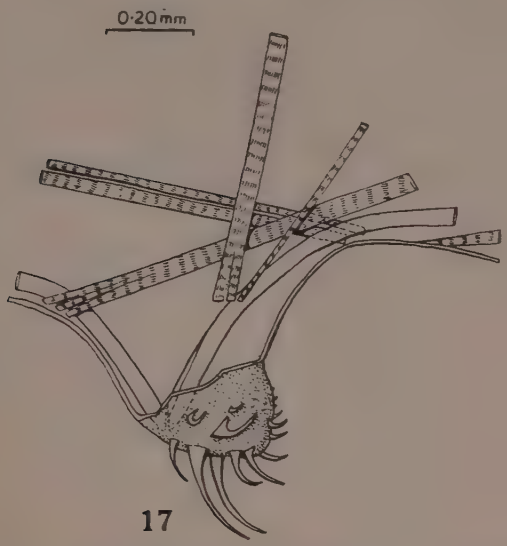


FIG. 17.—*Ephydra riparia* Fallén. Outer view of left proleg of the fifth abdominal segment of the mature larva. The proleg retractors are unshaded.

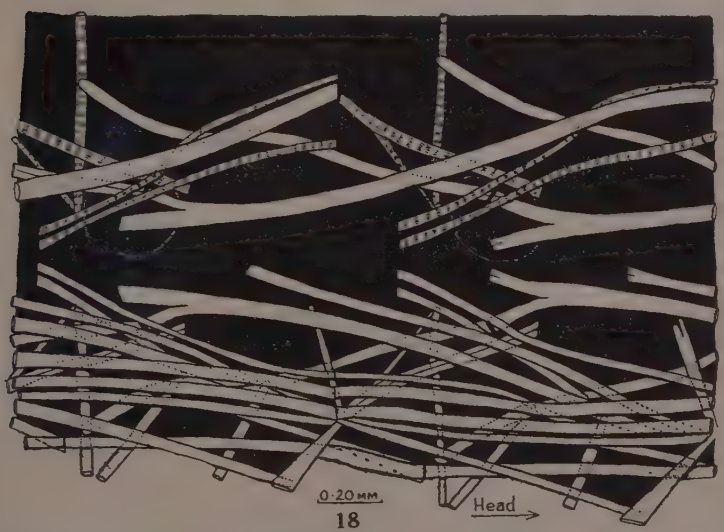
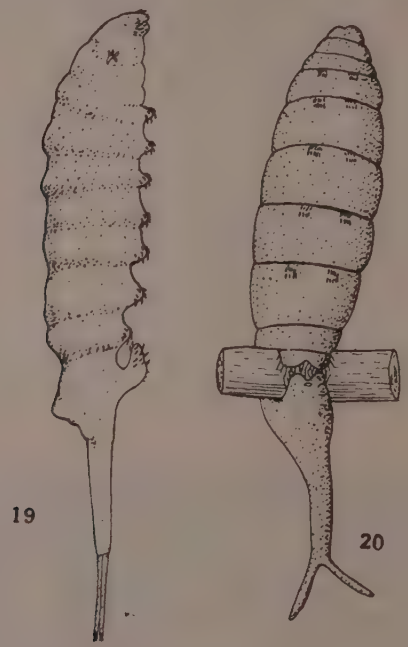


FIG. 18.—*Ephydra riparia* Fallén, mature larva. Inner view of prolegs of third and fourth abdominal segments. On the left side only the proleg muscles are shown : the proleg retractors are unshaded and those muscles inserted on or near the base of the proleg are shaded. Compare with figs. 1 and 2 of Plate I.

are therefore living in a medium of a consistency not essentially different from that of liquifying fungi or other vegetable matter, notwithstanding the fact that above their actual environment there may be several feet of water. Owing to the low oxygen tension of their environment the larvae must take their chief supply of oxygen from the intercellular air-spaces of roots and stems. These roots and stems provide a firm support on which prolegs could be used, but owing to the restriction of movement imposed on the larvae by their particular



FIGS. 19, 20.—(19) Larva of *Ephydra subopaca* Loew (after Ping). (20) Puparium of *Ephydra riparia* Fallén (after Keilin).

method of securing oxygen it may be supposed that the selective value of prolegs has dropped below that necessary to preserve them. In contrast, the Syrphidae (p. 493) secure their oxygen in such a way that they are left free to move on the firm substrate at the bottom of environments of liquid or semi-liquid organic matter, and their prolegs are retained.

(xviii) *Canaceidae.*

Canace Hal. and allied genera are usually included in the family Ephydridae. Most or all are phytophagous. The only one I have bred, the intertidal *Canace nasica* Hal., feeds on marine algae. It lacks prolegs, but the intertidal *Canace nudata* Cresson of Hawaii and the Pacific coast of N. America has an unpaired ventral, crochet-bearing proleg on the eighth abdominal segment, as has the

freshwater *Procanace nigroviridis* Cresson of Hawaii (Williams, 1938). It is very probable that the proleg of *Canace* and *Procanace* and those of *Ephydra* and its close relatives have been evolved independently.

(xix) *Sciomyzidae.*

Very little is known of the biology of this family. The larvae that have been described are aquatic and amphipneustic or, e.g. some *Tetanocera* Dum., metapneustic. Many of the species are probably saprophagous, but *Colobaea* Zett. and *Ctenulus* Rond. have been found in freshwater snails (*Limnea*, *Planobis*) where they also pupate. It has been suggested that these may be parasitic on the snails. According to the summaries of Johannsen (1935) and Wesenburg-Lund (1943) the larva of *Sepedon* Latr., that lives near the surface among *Limnea* and other aquatic plants, has a transverse row of prolegs at the anterior margin of each of the first seven abdominal segments. The larvae of *Tetanocera* Dum. and *Dictya* Meig. are said to resemble those of *Sepedon*, and they also live near the surface among aquatic plants.

The prolegs of the Sciomyzidae are a further example of the independent evolution of these structures in the Diptera. The families to which the Sciomyzidae are most closely related have non-aquatic larvae without prolegs.

(xx) *Calliphoridae.*

The larvae of this family are carnivorous or saprophagous and usually live in decaying animal or vegetable matter. Most of the species have transverse creeping welts on the thorax and abdomen. Significantly enough, the only known aquatic species is apparently also the only species with prolegs. *Wilhelmina nepenthicola* Vill. lives in the water of pitcher plants of the genus *Nepenthes* in the East Indies. According to Johannsen (1935), it has many pairs of ventral prolegs. There can be no doubt that the prolegs of this species have been evolved independently of those of any other dipterous larva.

In at least some of the species of *Protocalliphora* that live in birds' nests and suck the blood of the nestlings, a sucker has been evolved on the thorax by means of which the larva attaches itself to its host. So far as I know, the only other dipterous larvae in which distinct suckers are evolved are aquatic forms, such as the Blepharoceridae and Psychodidae, in which the suckers function to hold the larva to the substrate.

(xxi) *Muscidae* (= *Anthomyidae*).

The distribution of prolegs in this very large family provides clear evidence of the secondary nature of these structures and of the kind of environmental conditions that lead to their development.

The larvae are predaceous, parasitic, saprophagous and phytophagous. In general form they are nearly all very similar. The body is round or broadly oval in cross-section, strongly narrowed anteriorly, and the eighth segment is more or less broadly rounded behind. In non-aquatic forms a complete or incomplete transverse creeping welt with numerous crochets is present near the anterior margin of some or all of the abdominal segments. Somewhat less frequently similar welts are present on the thoracic segments.

Very few species are known to be subaquatic or aquatic, and prolegs are present in every one of these but in not one of the large number of species definitely known to be terrestrial. The species specialised for an aquatic existence belong to four different subfamilies: Muscinae, Phaoniinae, Lispinae and Mydaeinae. Whatever views are held on the proper classification of subfamilies within the Muscidae, it can hardly be supposed that the aquatic representatives of these four different groups have not invaded water independently, each being more closely related to certain existing terrestrial forms than to the other groups of aquatic Muscidae. In other words, prolegs have been evolved independently on at least four occasions within the family, each time in response to an aquatic or semi-aquatic environment. So far as I know, all are amphipneustic, like their terrestrial relatives, which argues for a relatively recent invasion of water by each.

Graphomyia maculata Scop. (Muscinae) has a pair of ventral prolegs on the second to seventh abdominal segment. It is found in the same kind of environment as *Eristalis* and *Ptychoptera* (Keilin, 1917).

In the Phaoniinae the aquatic species belong to the genus *Phaonia* (*S. lat.*). This is a very large genus of which the great majority of species are terrestrial. In Europe *P. keilini* Collin and *P. mirabilis* Ringd. are found in water in tree-boles. According to Tate (1935), the larva of *P. mirabilis* also uses its prolegs in catching the mosquito larvae on which it feeds. Both species have a pair of ventral prolegs on the second to eighth abdominal segments. *P. nepenthincola* Stein. is found in Java in the water of pitcher-plants of the genus *Nepenthes* (de Meijere, 1910). It has ventral abdominal prolegs, but from de Meijere's account I am not certain of their exact number. Descriptions and figures of a number of terrestrial species that live in decaying vegetable and animal matter are given by Keilin (1917). Thompson (1937) has illustrated *P. variegata* Meig., which feed on Mycetophilids in *Polyporus* and has creeping welts somewhat like those of its prey. When more is known of the genus *Phaonia* it may be possible to show that some of the species that are now aquatic have become so and developed prolegs independently of others. For instance, I think the European *P. keilini* and *P. mirabilis* are probably more closely allied to some of the European terrestrial species than they are to *P. nepenthincola* of Java.

Among the Lispinae, two Hawaiian species, *Lispocephala fusca* Mall. and *Lispe metatarsalis* Thoms., are known to live in very damp places, often actually beneath the surface of the water (Williams, 1938). *Lispocephala fusca* has a pair of crochet-bearing prolegs on abdominal segments 2–8, and *Lispe metatarsalis* has paired prolegs on segments 2–6 at least.

In the Mydaeinae, the larvae of *Limnophora riparia* Fall. (= *Melanochelia riparia*) of Europe are found in moss over which the stream is flowing rapidly. They are particularly common when the water is spilling over a steeply inclined or vertical face. According to Johannsen (1935), *Limnophora aequifrons* Stein., *L. torreyae* John. and other North American species are aquatic as well as *Mydaeina* Malloch. All of the aquatic species are predaceous, as are the aquatic Muscids previously mentioned. All have prolegs. In *Limnophora* there is a pair of ventral prolegs on segments 2–8 of the abdomen. The anterior prolegs are small, but those of the eighth segments are exceptionally long and always curved forwards. The six anterior pairs of prolegs have retractor muscles inserted in their apices, but in the posterior pair the most distal insertions are

behind the apical third of the proleg. All other dipterous prolegs that I have examined have retractors inserted in their apices.

B. Lepidoptera.

1. General considerations.

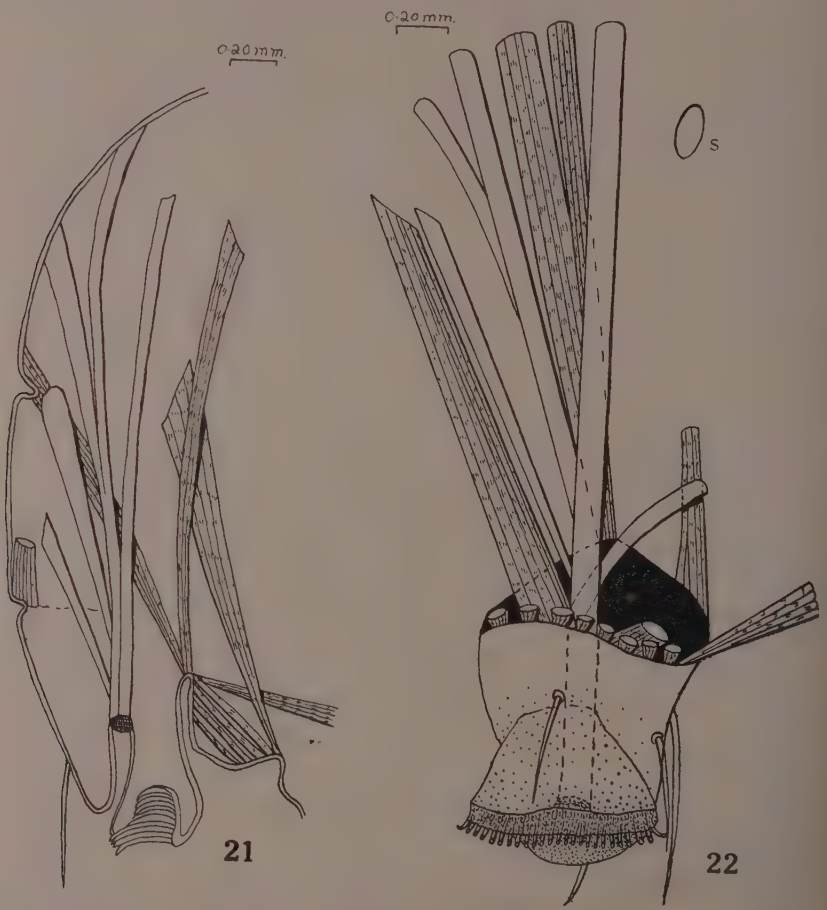
The morphology of the larval prolegs has received very little attention from a comparative point of view, although the external form of a considerable range of species is described by Goossens (1887). Schultze (1920) has described in some detail the variations in the number and form of the crochets of several species. The many other studies that have been made are restricted to single genera or families ; and apart from isolated accounts of single species and a few very general studies, such as that of Snodgrass (1935), nothing is known of their internal structure except for a short comparative account of their musculature by Hinton (1952). For this reason, therefore, it is not surprising to find it widely held that the groups that have prolegs adapted for climbing are monophyletic, a view that has unfortunately greatly influenced some recently proposed classifications of the order, such as that of Kiriakoff (1948).

2. The structure of the prolegs

The prolegs of the third to sixth abdominal segments will be referred to as the ventral prolegs and those of the tenth as the anal, although the latter are also ventral. The ventral prolegs are hollow cylindrical outgrowths of the body wall. In most Microlepidoptera (Monotrysia and Ditrysia) and in the early instars of all and the final instar of some Papilionoidea they have a complete or nearly complete apical circle of strongly sclerotised curved hooks known as crochets. The lumen of each proleg is continuous with the haemocoele. The apical area bounded by and bearing the crochets is membranous and much less rigid than the sides of the prolegs. It is known as the planta. The retractor muscles are inserted in the planta, usually in its centre. The central part of the planta on which the muscles are inserted is often distinctly sclerotised, as it usually is in the highly specialised Ditrysia (figs. 21–22). The retractor muscles arise on the body wall more or less directly above the proleg. They consist of a variable number of separate groups of fibres. In most of the families that were examined, they consist of two distinct sets, one arising well below and the other above the spiracle, as in the Cossidae. In the Hepialidae (*Hepialus*) and Yponomeutidae (*Yponomeuta*), however, all of the planta retractors arise above the level of the spiracle.

Contraction of the retractor muscles pulls the centre of the planta inwards, and the whole of the planta may be more or less completely invaginated within the proleg. The crochets on the periphery of the planta have their apices directed outwards and upwards. They are attached to the cuticle of the planta for about one-half to three-fourths of their lengths in such a way that when the planta is pulled inwards against turgor pressure they are so tilted that their apices, instead of projecting upwards, now project ventrally and are more or less parallel to the long axis of the proleg. Thus by retraction of the planta the crochets are disengaged. They are engaged again when the retractors are relaxed and turgor pressure evaginates the planta. The caterpillar therefore always pulls the planta inwards before shifting the position of the proleg.

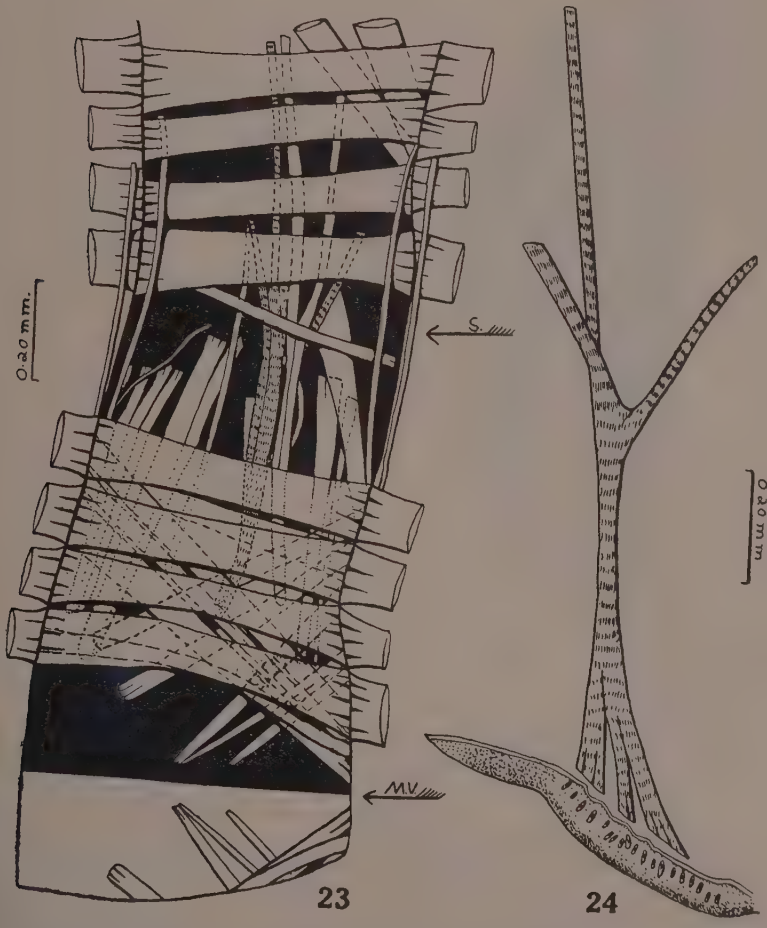
Ripley (1923) claims that in the Phalaenidae muscles are inserted in the proximal ends of the crochets, but this is not so, either in that or related families. Species belonging to all of the principal superfamilies of the order have been examined, and in no case were muscles inserted in the crochets themselves.



FIGS. 21, 22.—*Polia nebulosa* Hufn., mature larva. (21) Cross section through left side of fifth abdominal segment to show proleg, which is considerably retracted. (22) Inner side of left proleg of fifth abdominal segment as seen when protracted. Proleg retractors are unshaded and basal muscles of proleg are shaded. (*S*) Spiracle.

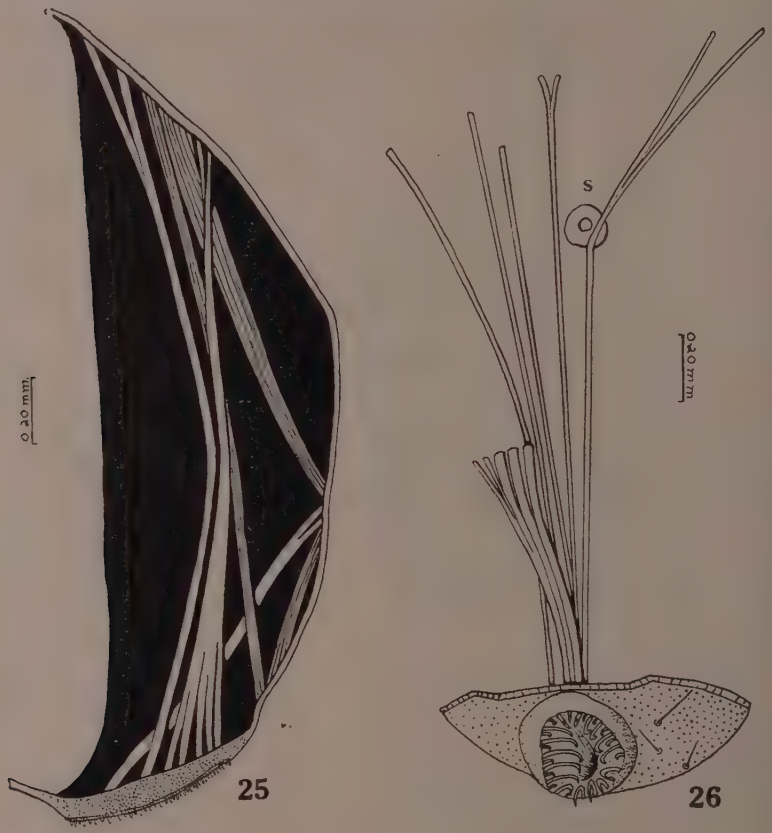
Movements of the prolegs, other than retraction or evagination, are effected by variations of turgor pressure and by the muscles inserted in the body wall near their bases. The areas of the body wall adjoining those that give rise to the prolegs have numerous transverse, oblique and longitudinal muscles as shown, for instance, in fig. 23.

It is probable that the retractors of the planta are, as in the Diptera, merely slightly specialised muscles of the body wall. The body wall is richly supplied with transverse (dorso-ventral) muscles so that wherever an outgrowth or protuberance of one kind or another is evolved, muscles are present that, by a slight increase in their lengths or a slight adjustment in their positions, can become retractors of the newly evolved outgrowth. Among the most simple ventral prolegs are those of the Adelidae (figs. 23–24). Whether this simplicity is brought about by reduction from a more complex proleg or whether it is



FIGS. 23, 24.—*Adela* sp., mature larva. (23) Complete musculature of right side of fourth abdominal segment. The retractor muscles of the proleg are shaded. (24) Posterior view of left proleg of sixth abdominal segment. (*M.V.*) Mid-ventral line. (*S.*) Level of spiracle; the slender diagonal muscle shown at this level is the occlusor of the spiracle.

primitive is discussed on p. 509–510. The prolegs of the Adelidae differ little in structure from the transverse creeping welts of the Diptera, and it seems certain that they resemble a stage in the evolution of prolegs from structures like creeping welts even though they may not actually be one.



Figs. 25, 26.—(25) *Nymphula nymphaeata* L., mature larva. Cross section of right side of fifth abdominal segment to show the muscles of the proleg. (26) *Nymphula stratiotata* L., mature larva. Outer view of left proleg of sixth abdominal segment. (*S*) Spiracle.

The ventral prolegs of the Zygaenidae, many Papilionoidea, Geometriidae, Phalaenoidea, Bombycoidea, Saturnoidea and Sphingidae are modified in a very characteristic fashion that enables them to cling to thin twigs with a force not possible to larvae of comparable size that have prolegs of the primitive type. When the larva is at rest, the twig is clasped between the prolegs in such a way that, if narrow enough, the prolegs may completely embrace it. At first sight it appears that this type of proleg is especially adapted for climbing about on plants. This impression receives support from the fact that it is the

type found in all of the exclusively arboreal caterpillars that move about freely exposed and do not live in shelters of some kind as do the Microlepidoptera. Furthermore, the only terrestrial or semi-terrestrial larvae that have this kind of proleg are species of Phalaenoidea that can be shown in each case to be secondarily terrestrial (see p. 515).

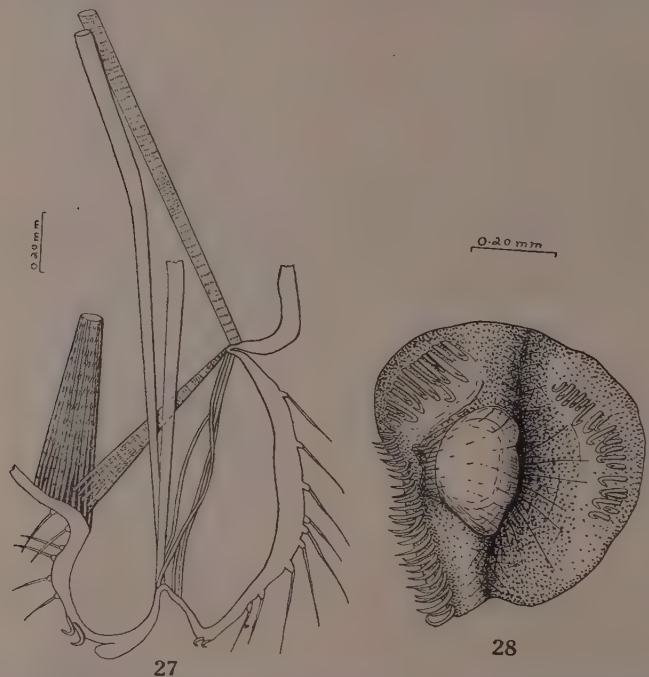
Each of these specialised prolegs is somewhat tilted mesally towards the other of the same pair. The crochets, which do not differ in structure from those of the primitive type of proleg, are restricted to a straight or sinuate longitudinal line on the mesal side of the planta only. This arrangement of crochets is known as a mesoseries, and each crochet has its apex curved mesally and upwards. The planta is retracted and everted as in the Microlepidoptera. The retractor muscles often also consist of two sets, one arising on the body wall directly above the proleg dorsal to the spiracle and the other ventral to the spiracle (fig. 22), as in the Zygaenidae, Lycaenidae, Phalaenidae, Arctiidae and Sphingidae. The centre of the planta in which the retractor muscles are inserted is, of course, always laterad from the crochets.

As in the primitive proleg, the crochets of the specialised type are disengaged when the planta is pulled inwards, but the action of the proleg as a whole is much more complex. A variable number of muscles are inserted on the base of the proleg itself (figs. 21–22, 27), and in some groups, e.g. the Geometriidae, muscles that arise near the spiracle are inserted on its middle outer face. Furthermore, there may be, as in the Geometriidae, a specialised ventral musculature between the two prolegs of a pair. For instance, among the few Geometriidae examined three obviously different patterns of ventral muscles were present, one of these including muscles that extended between the inner bases of the right and left prolegs.

The way in which the primitive type of proleg present in most Microlepidoptera was altered to become a specialised climbing organ is clear from a study of larval development in almost any of the Papilionoidea except some Hesperidae and Papilionidae. As I have previously shown (Hinton, 1946), the first instar of all Papilionoidea has a primitive type of proleg with a complete circle of crochets. In successive larval instars of most species, the crochets on the outer side of the planta become less numerous and smaller relative to those of the inner side at each moult until, in the mature larva, they are lost altogether and only the mesal crochets are left to form a typical mesoseries. In the final instar of some Lycaenidae the process is not quite completed, and some of the outer crochets are still present (fig. 28). In the more specialised arboreal caterpillars, e.g. Sphingidae, Saturnoidea, Bombycoidea and most Geometriidae and Phalaenoidea there is no ontogenetic sequence of this kind, and a mesoseries is already present in the first instar.

The ventral prolegs do not closely resemble, even superficially, the thoracic legs, but, in so far as they do, it is significant that it is the prolegs of the most highly specialised species that do so. The prolegs of primitive larvae in no way resemble legs, but it is precisely these that would most resemble legs if the theory that they are of the same series as the thoracic legs were correct. A few of the highly specialised arboreal and shrub inhabiting species, e.g. *Stauropus fagi* L., have superficially 2-segmented prolegs. However, as has already been shown, both the environment that these species now occupy and the structure of their prolegs is clearly secondary.

The anal prolegs are structurally similar to the ventral, but in no known species is there a complete circle of crochets, the circle always being incomplete posteriorly. Of the species that I have examined, it is most complete in the Psychidae. As a general rule, the number of planta retractors is greater in the anal than in the ventral prolegs. In many species, as in the Pyralid shown in fig. 29, the planta retractors are inserted over a wide area of the planta and are not concentrated at one point, as they apparently always are in the ventral prolegs except in some of those of the Incurvaroidea. The anal prolegs of at



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Figs. 27, 28.—*Strymon w-album* Knoch, mature larva. (27) Longitudinal section through the right proleg of the sixth abdominal segment. The retractor muscles of the proleg are unshaded. (28) Ventral view of apex of the right proleg of the sixth abdominal segment.

least some species of *Hepialus*, e.g. *H. lupulinus* L., are unusual in that the apex of each proleg is more or less subdivided, and each part has its semicircle of crochets. In these species there are two distinct groups of planta retractors, one to each subdivision, as well as a retractor inserted in the apical membrane between the subdivisions.

The anal prolegs of the specialised climbing larvae, in which the crochets of the ventral prolegs form a mesoseries, are usually very similar in structure to the ventral prolegs. The prolegs usually have only a straight or sinuate line of crochets, and they are so formed that the line is parallel or oblique to the long axis of the body with the apices of the crochets curved mesally and upwards.

The curved line or semicircle of crochets of the anal prolegs of primitive larvae is at right angles to the long axis of the body. The anal prolegs of climbing larvae are clearly adapted for climbing in approximately the same way as are the ventral prolegs.

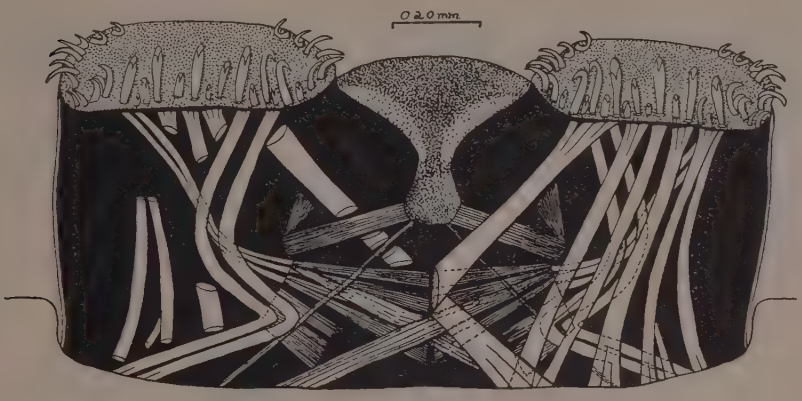

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FIG. 29.—*Nymphula stratiotata* L., mature larva. Musculature of the prolegs of the tenth abdominal segment. The retractors of the prolegs are unshaded.

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FIG. 30.—*Polia* sp. (Phalaenidae), mature larva. Musculature of the prolegs of the tenth abdominal segment. The retractors of the prolegs are unshaded.

In all species examined, the planta retractors were more or less contiguous, usually on a distinctly sclerotised circular area of the planta (fig. 30). In the Phalaenoidea, judging from the Phalaenidae and Arctiidae examined, there are no other proleg muscles, but the truth of this statement depends on how the proleg is delimited. Its proximal part is often not clearly differentiated from the remainder of the tenth segment, the central area of which has a very

characteristic transverse bridge of muscles (fig. 30) and some others besides. Some of the latter might be considered to be basal retractors of the prolegs. However this may be, in other groups of climbing larvae, e.g. Geometriidae (fig. 31), Lasiocampidae, Bombycidae and Sphingidae, many other muscles are inserted on the base and inner sides of the prolegs. These specialised climbing larvae also often have intrinsic proleg muscles, e.g. *Bombyx*, *Deilephila*, and many, if not all, Geometriidae (fig. 31). Most of the additional muscles evolved by climbing forms are so orientated that on contraction they increase the clasping force of the prolegs.

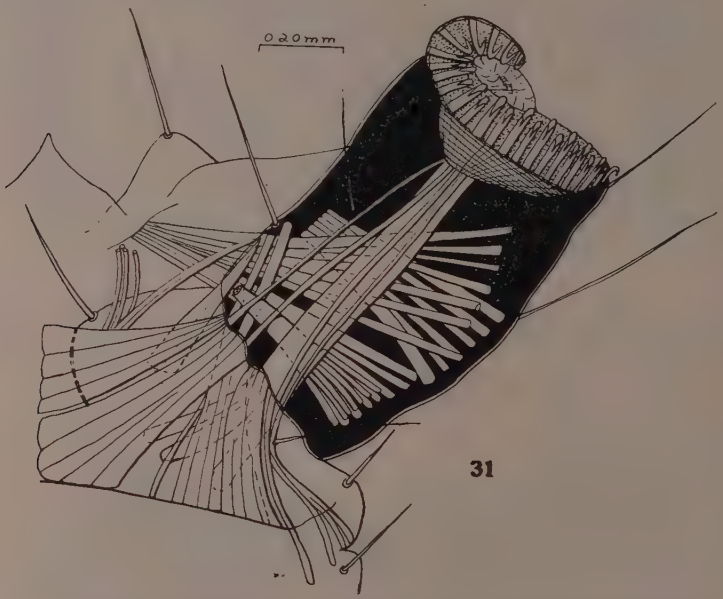

Fig. 31.—Geometrid sp., mature larva. Ventral view of proleg of tenth abdominal segment.

When the prolegs of climbing forms are much reduced or modified to subserve other functions, their muscles may be reduced or lost. For instance, such Notodontidae as *Stauropus fagi* L., that have very long anal prolegs adapted for defence, now lack both the planta retractors and any other muscles they may once have had. The anal prolegs of these are moved entirely by muscles inserted on the sternal areas around their bases and by variations in turgor pressure. Other Notodontidae, such as *Cerura vinula* L., that have the anal prolegs adapted in another way for defence, still retain planta retractors.

Both the ventral and anal prolegs that are modified as climbing organs are, except for differences in their muscles other than planta retractors, remarkably similar in structure and appearance notwithstanding the fact that they have been independently evolved many times from a proleg like that of recent Microlepidoptera. This type of proleg has been independently evolved in the

Zygaenidae, Papilionoidea, Geometriidae, Phalaenoidea, Sphingidae and in the Bombycoidea-Saturnoidea. Furthermore, it seems certain that it has been independently evolved at least three times within the Papilionoidea and may have been evolved several times in the series Bombycoidea-Saturnoidea. In short, it seems certain that a climbing type of proleg has been evolved no less than eight times within the Lepidoptera.

The planta of the prolegs may sometimes function as a sucker when the larva is crawling on a smooth hard surface. At such times, as noted by Snodgrass (1935), the crochets are turned upwards and the planta is pressed against the surface so that its fleshy periphery inside the line of crochets seals a central hollow. In this position a slight contraction of the planta retractors increases the volume of the central hollow without admitting air, and thus, by lowering the internal pressure, the central hollow functions as a vacuum cup. In some caterpillars, e.g. some Lycaenidae (figs. 27–28), there is a fleshy lobe between the centre of the planta and the mesal crochets. This lobe appears to function as an adhesive organ, and it is possible that a gland or glands may open on it.

(a) 3. Reduction and loss of prolegs

Most lepidopterous larvae have a pair of crochet-bearing prolegs on segments 3–6 and 10 of the abdomen. With the possible exception of the Eriocraniidae, all larvae that have a different complement of prolegs, or that have none, can be shown to be evolved from groups that had prolegs on segments 3–6 and 10. For this reason it seems probable that the ancestor of all recent Lepidoptera had crochet-bearing prolegs on segments 3–6 and 10 of the abdomen.

Larvae of a number of families have other than the primitive complement of prolegs. This is also true of a number of species and genera that belong to families in which most species have the primitive number and arrangement of prolegs. Prolegs are reduced or lost in both free-living and mining larvae. Most of the miners are leaf-miners.

The prolegs of the tenth segment are sometimes lost in leaf-miners that retain those of segments 3–6, viz. in the Incurvariidae and Adelidae, the species of which are usually leaf-miners in the first instar only. Among the free-living forms that have prolegs on segments 3–6, those of the tenth segment are apparently lost only in Drepanidae, some Notodontidae, and are said to be lost in some Syntomidae. Many of the Notodontidae have the last pair of prolegs modified to subserve other functions, and in these species they are no longer used for walking. The reduction and loss of the prolegs of segments 3–6 of free-living and leaf-mining larvae differs in some features. In free-living larvae the prolegs of the third, fourth and fifth segments are the first to be lost; and those of the third segment are always lost before or at the same time as, but never after, those of the fourth. Similarly, those of the fourth segment are lost before or simultaneously with those of the fifth. Furthermore, as the anterior 1–3 pairs of prolegs are reduced or lost, the remaining prolegs become larger and stronger. In leaf-miners, on the other hand, the prolegs of segments 3–6 are reduced or lost simultaneously except in the tissue- or non-feeding instars of most Lithocolletidae and in the second and following instars of some Coleophoridae, in both of which only the prolegs of the sixth segment are lost.

(i) *Reduction or Loss of Prolegs in Leaf-miners.*

A reduction in the size and complexity of both prolegs and legs, or even their total loss, is one of the most characteristic adaptive modifications undergone by leaf-mining larvae. For instance, thoracic legs are sometimes reduced in other Lepidoptera but they are entirely lost only in miners. Except for the free-living Eucleidae, the only larvae that have lost all abdominal prolegs are miners, although in many others the number of prolegs may be reduced, sometimes to as few as two pairs, e.g. many Geometridae. The leaf-mining larvae of the Ditrysia that have either no prolegs or poorly developed ones can be derived in all instances from groups with well-developed crochet-bearing prolegs on segments 3–6 and 10 of the abdomen. For this reason a poorly developed proleg is said to be reduced, and, when none are present, they are said to be secondarily lost. In this respect the Monotrysia are similar to the Ditrysia, but it is just possible that the absence of prolegs in the Dacnonypha is not secondary.

Species that are leaf-miners during only part of their larval life are always leaf-miners in their early instars and never in their later instars. The absolute size of the partly or full-grown larva of many species may, of itself, preclude it from becoming a leaf-miner in the leaves of its host plant. Among other factors that have determined such an ontogenetic sequence of habits may be mentioned the relatively more delicate and defenceless early instars for which life in a leaf-mine may have a greater selective value than for the larger and stronger larvae. The particular ontogenetic sequence of habits to which I have referred, is, in many larvae, reflected at a morphological level; and in species in which crochets, or both crochets and prolegs, are reduced or lost in some instars but not in others, they are without exception reduced or lost in the early instars.

(a) *Eriocraniidae.*

The only larvae known of the most primitive suborder, the Dacnonypha, are those of the Eriocraniidae. All Eriocraniid larvae are leaf-miners, and none have legs or prolegs. The absence of thoracic legs is secondary as is shown by the fact that larvae of Panorpoidea more primitive than the Lepidoptera have legs together with the fact that nearly all the larvae of much more specialised Lepidoptera have legs. The larvae of the Monotrysia and Ditrysia that are also leaf-miners have often also lost their legs. The absence of abdominal prolegs in Eriocraniid larvae does not necessarily mean that within the Lepidoptera these structures were first evolved in the Monotrysia. It is probable, but not quite certain, that the ancestral Eriocraniid had the normal lepidopterous complement of prolegs, and that their present absence is one result of their specialised habit of leaf-mining. The only Lepidoptera that have lost thoracic legs are leaf-miners and *Prodoxus* (Prodoxidae), which mine in the fruit and fruit-stalk of *Yucca*. By analogy with other groups of leaf-miners it is clear that as a result of leaf-mining both legs and prolegs tend to be reduced or lost. It is also quite clear that prolegs are lost before legs, and no larva is known with ventral or anal prolegs but without legs. It is therefore reasonable to suppose that if the ancestral Eriocraniid had prolegs these would have been lost before their thoracic legs were completely lost.

(b) *Incurvariidae* (=*Lamproniidae*) *and Adelidae.*

The genera related to *Adela* Latr. were given subfamily rank within the Incurvariidae by Spuler (1910). Forbes (1923) included *Adela* and its allies in the Incurvariidae. More recently the Adelinae have been given family rank. The habits and structure of the immature stages of both groups show that they are very closely related, and they are here treated as one family.

The larvae of most of the species that have been studied are leaf-miners in their first instar. They later live in portable cases fashioned from pieces of leaves. Many of these live on the ground and feed on fallen leaves. Others, e.g. *Paraclemensia acerifoliella* Fitch, are case-bearers on the upper or lower surfaces of the leaves of their host plant. A few species, e.g. *Phylloporia bistrigella* Haw., are leaf-miners until mature, when they cut out a case from the mine and descend to the ground to pupate. *Lampronia capitella* Clerck burrows in the young shoots and stems of *Ribes* in all instars, and *L. rubiella* Bjerk. burrows in its first instar in the fruit receptacles of raspberry and in later instars in the shoots. In the Adelinae, the first instar of *Adela* and *Nemophora* Hofm. burrows in flower-heads and seed capsules, and the first instar of *Nematopogon* Zell. is a leaf-miner. In later instars the larvae of all three genera are case-bearers on the ground.

Both the Incurvariinae and Adelinae that are leaf-miners, or bore into flower-heads in their first instar and later become case-bearers, have in the case-bearing instars one (*Incurvaria* Haw.), or several (Adelinae), transverse rows of small crochets on each of the wide and very short prolegs of segments 3–6. The tenth abdominal segment is bilobed beneath but functional prolegs are lost. According to Chapman (1893), the later instars of both *Nemophora fasciella F.* and *Adela rufimetrella* Scop. have prolegs with crochets on the tenth abdominal segment. Dampf (1910) and Forbes (1910) have shown that *Nemophora degeerella* L. lacks prolegs and crochets on the tenth abdominal segment. *Adela reaumurella* L. (Fracker, 1915) and undetermined species of both *Nemophora* and *Adela* that I have examined also lack functional prolegs and crochets on the tenth segment. For these reasons it seems possible that neither prolegs nor crochets were present in the species studied by Chapman.

The mature larva of *Lampronia rubiella* Bjerk. has moderately large prolegs on segments 3–6 and 10 of the abdomen[9] but these are without crochets. I have not seen the first instar of this species, but it is fairly certain that it too lacks crochets if, indeed, it has prolegs, since in the whole order there is no known species that has crochets in its early instars but loses them in its later ones. According to Chapman (1893), the young larva of *Lampronia capitella* Clerck lacks crochets, but by the time it is full grown a nearly complete circle of crochets is present on each proleg.

Chapman (1893), Forbes (1910), and others believe that the particular condition of the prolegs and crochets of *Incurvaria* and *Nemophora* illustrate some of the stages in the evolution of these structures, although they admit that the prolegs and crochets of these genera are secondarily reduced. Organs that are specialised in the direction of reduction (i.e. simplicity of organisation) may come to resemble particular stages through which they passed before they

[9] The only specimen I have seen is damaged in such a way that I cannot be certain that it has prolegs on the tenth segment, but it certainly has no crochets on this segment.

reached the organisational level from which they are now evolving in the direction of simplicity. Since neither the morphological pre-history of the organ nor the pre-history of the relation between the animal and its environment is the same at these two different stages, morphological similarities provide no evidence of the past or future condition of the organs being compared. For instance, the resemblance between the simple worm-like body of some fly larvae to that of the annelid-like ancestor of the Arthropods provides no clue to the morphological changes undergone by either, although the similarity of form may indicate some similarity in the relation each establishes with its environment.

It is not easy to account for the loss of functional prolegs on the tenth abdominal segment of the case-bearing Incurvariidae and Adelidae. A more careful study than has yet been made of the movements of the larvae within their cases may suggest an explanation. The anal prolegs are never lost in any other lepidopterous larvae that have portable cases, nor are they lost in any species of the order Trichoptera, most of which are case-bearers. Some of the Tineidae construct cases very similar to those of the Incurvarioidea, and the larvae of some species are also able to turn around within the case and use either end as the cephalic opening.

The loss of the anal prolegs in *Incurvaria* and *Nemophora* could be explained on the assumption that the ancestor of each was a leaf-miner in all instars. It is necessary to suppose that these genera are evolved from forms that were miners in all instars, since the anal prolegs are lost in all, and, by analogy with other groups, it is evident that changes in the relation of the larva to its environment affect, at any rate at a morphological level, only the instars concerned. If such an assumption were correct, the condition of the prolegs of segments 3–6 of *Incurvaria* and *Nemophora* probably illustrates some of the stages in the evolution of prolegs and crochets by the common ancestor of the order.

A corollary of the assumption that a total loss of prolegs occurred in the ancestor of both *Incurvaria* and *Nemophora* is that prolegs have been independently evolved thrice in the Lepidoptera, once in the common ancestor of the order and once in each of the above mentioned genera or their immediate ancestors.

(c) *Prodoxidae.*

The larvae of the two genera, *Prodoxus* Riley and *Tegeticula* Zell., included in this family differ as regards legs and prolegs. *Tegeticula yuccasella* Riley feeds on the seeds in the developing ovaries of *Yucca* flowers. Its legs are present but much reduced. According to Riley (1892) prolegs are absent, but Fracker (1915) and Forbes (1923) claim that feebly developed prolegs without crochets are present on segments 3–6 of the abdomen. The species of *Prodoxus*, e.g. *P. quinquepunctella* Chamb., feed in the flesh of the fruit or fruit stalk of *Yucca*, and writers are agreed that it lacks both legs and prolegs (Riley, 1892 ; Fracker, 1915).

(d) *Heliozelidae.*

The larvae are leaf-miners or gall-makers in all instars. They pupate in lenticular cases cut from the epidermis of the mine or gall. The pupal cases either fall to the ground or are attached by the larvae to twigs. Some species

are known to carry their cases some distance before pupating, e.g. *Coptodisca splendoriferella* Clem. According to Snodgrass (1922), this species has a pair of oval colourless areas that function as an adhesive disc on the tergites and sternites of the meso- and metathorax and the eighth abdominal segment. Similar but transversely elongate areas are present on the sternites of the third to sixth abdominal segments. The ventral adhesive discs or suckers are used when the mature larva crawls away with its pupal case. Both dorsal and ventral suckers are used in moving in the mine. Snodgrass suggests that the larva can maintain a fixed position in the mine by using the suckers as adjustable hydraulic wedges. The suckers are evidently a secondary and not a primitive feature in the family, and they were probably evolved after the loss of both legs and prolegs.

(e) *Stigmellidae* (= *Nepticulidae*).

The larvae are leaf-miners in all instars. Legs and prolegs are lost in all known species, but a pair of ventral non-retractile protuberances is present on the meso- and metathorax as well as on each of abdominal segments 2–7. The distribution on the abdomen of these protuberances, which may function as ambulatory warts, suggests that they may have been evolved after both legs and prolegs were lost. The leaf-mining larvae of the related family Opostegidae are similar but apparently lack the ambulatory warts of the Stigmellidae.

(f) *Tischeriidae.*

The larvae are leaf-miners in all instars. Some species are said to have no thoracic legs (Fracker, 1915 ; Grandi, 1929), but Jayewickreme (1940) claims that legs reduced to minute protuberances were present in the species he examined. Feebly developed crochet-bearing prolegs are present on abdominal segments 3–6 and 10 in *Tischeria guanacella* Dup. and *T. heinemanni* Wck. (Grandi, 1929, 1933), but both prolegs and crochets are said to be absent except on the tenth segment of *T. complanella* Hb. (Jayewickreme, 1940). The reduction or actual loss of legs and prolegs in some Tischeriidae is clearly secondary.

(g) *Lithocolletidae* (= *Gracilariidae*).

The larvae of nearly all Lithocolletidae are leaf-miners at least in their early instars. Most of the species undergo a distinct hypermetamorphosis. The first two or more instars feed on sap, but usually at the second or third moult the shape of the body and the structure of the mouth-parts is considerably altered, and the larva begins to feed on the parenchyma. At this time some species leave the mine and make a nest on the leaf, usually by rolling over the end. Some highly specialised forms, e.g. some species of *Marmara* Clem., feed only in the first phase. The larva then moults but does not shed the cuticle of the previous instar. A further moult then occurs and the cuticles of the two previous instars are shed simultaneously and the larva, again without feeding, spins a cocoon. The change from the sap-feeding to the tissue-feeding phases may be gradual and take two or three moults, as in some species of *Acrocercops* Wallen.

The sap-feeding instars of species of *Lithocolletis* (*L. concomitella* Bankes, *L. platani* Stgr., *L. pastorella* Zell., *L. corylifoliella* Haw., etc.) are apodous (Grandi, 1933 ; Jayewickreme, 1940), but in their tissue-feeding instars have legs as well as crochet-bearing prolegs on segments 3–5 and 10 of the abdomen. *Gracil-*

laria syringella F., *Ornix avellanella* Staint. (Jayewickreme, 1940), and many other Lithocolletidae are similar. However, some species, e.g. *Gracillaria* (*Parectopa*) *latifoliella* Mill., are apodous in all instars (Grandi, 1933). The absence of legs and prolegs in the early instars of *Lithocolletis* and *Ornix* and their presence in later instars is not a recapitulative sequence, since the common ancestor of the Lithocolletidae and other Ditrysia was not apodous but had thoracic legs as well as prolegs on segments 3–6 and 10. The retention of legs and prolegs in the latter instars would appear to be due to the less specialised habits of these instars. After their sap-feeding instars, most species leave their mines and live in a nest on the surface of the leaf. Some other species of the family, such as *G.* (*P.*) *latifoliella* Mill., that do not leave their mines in later instars, are apodous in all instars.

(h) *Phyllocnistidae.*

This family includes only the genus *Phyllocnistis* Zell. which, by some writers, is given only subfamily rank within the Lithocolletidae. The larva of *P. citrella* Staint. has been described by Clausen (1931) and that of *P. suffusella* Zell. by Grandi (1933) and Jayewickreme (1940). The first three instars are active leaf-miners and have lost both the thoracic legs and the abdominal prolegs. The fourth instar is also apodous. It does not feed. It pupates in a partly folded edge of the mine. On the sides of the body of all instars there are small retractile protuberances that probably assist in locomotion. The protuberances or ambulatory warts are secondary or specialised structures. They never bear crochets. In the feeding instars of *P. suffusella* there is a pair on the meso- and metathorax, a pair on each of the first seven abdominal segments, and two pairs on the eighth, which are also lateral. In the fourth instar a pair of minute lateral protuberances is present on each of segments three to seven of the abdomen. On the pre-pupal larva of *P. citrella* Staint. a pair of similar protuberances is present on the fifth, sixth, and seventh abdominal segments.

(i) *Lyonetiidae.*

Good descriptions of various species have been given by Grandi (1933) and Jayewickreme (1940). All instars of some species, e.g. *Bedellia somnulentella* Zell., have crochet-bearing prolegs on segments 3–6 and 10 and also well developed thoracic legs. *B. somnulentella* is unusual in that the prolegs of the third and sixth segments are shorter than those of the fourth and fifth segments. *Lyonetia clerckella* L., *L. laburnella* Staint., and the species of *Leucoptera* Hb. (e.g. *L. lotella* Staint. and *L. scitella* Zell.) lack prolegs in their early instars but retain them on segments 3–6 and 10 in the later instars. Thoracic legs are present, but usually more or less reduced in the later instars. In the early instars they are sometimes absent, e.g. *Lyonetia clerckella* L. and *Leucoptera laburnella* Staint. The absence of prolegs in the early instars is to be interpreted as a secondary loss of these structures for the reasons given in the similar case of the Lithocolletidae.

(j) *Cosmopterygidae and Momphidae.*

Many of the species of both families are leaf-miners. Most of these leave their mines to pupate. The prolegs of many are said to be small, but most of the

available descriptions either do not mention the prolegs or do so unintelligibly. The mature larvae of *Cosmopteryx scribaiella* Zell. and *C. exima* Haw. (Grandi, 1933) have the normal complement of prolegs, all of which have crochets. In an unidentified species of *Mompha* Hb. described by Jayewickreme (1940) the prolegs are small, and those of the tenth segment have no crochets.

(k) *Gelechiidae.*

Nearly all the larvae of this family have well developed thoracic legs and crochet-bearing prolegs on segments 3–6 and 10 of the abdomen. Only a few species are leaf-miners or live inside seeds, and it is apparently only in these species that the prolegs and legs are appreciably reduced. *Aristotelia hermanella* F. (Jayewickreme, 1940) has four larval instars. The first instar lacks prolegs, and the thoracic legs are much reduced. In the second instar prolegs without crochets are present on 3–6 ; the prolegs of the tenth segment are indistinct or absent. In the third and fourth instars the prolegs of 3–6 have crochets, whereas those of 10 are small and without crochets. Thoracic legs are well developed in the second and following instars. Many other species of *Aristotelia* Hb. are not leaf-miners but live in rolled leaves or in a web between two leaves. These species all have crochet-bearing prolegs on 3–6 and 10. The last instar of *Nealyda pisoniae* Busck remains in its mine until it is ready to pupate. It is said (Busck, 1900) to have no prolegs on 10 but to have crochet-bearing prolegs on 3–6.

Metzneria lapella Zell., which feeds on the seeds in the burrs of burdock, and *Sitotroga cerealella* Oliv., which feeds inside the grains of various cereals, are said to lack prolegs (Fracker, 1915 ; Forbes, 1923). This requires confirmation, as it has been shown that the mature larva of *S. cerealella* Oliv. has small crochet-bearing prolegs on 3–6 and 10 (Hinton, 1943).

(l) *Coleophoridae.*

The first instar larvae of this family are always leaf-miners. After the first moult they live in portable cases made from pieces of the leaves on which they feed. Most of the species belong to the genus *Coleophora* Hb. In some of the species of *Coleophora*, e.g. *C. nigricella* Steph. (Jayewickreme, 1940), the leaf-mining first instar has anal prolegs but none on segments 3–6 of the abdomen. In the second and following instars prolegs are present on 3–5 but are absent on the sixth segment. In many other species the second and following instars have the primitive complement of prolegs. In others, e.g. *C. limosipenella* Dup. (Fracker, 1915), crochets and prolegs are lost on segments 3–6 of the abdomen.

(m) *Other leaf-mining Ditrysia.*

The families Plutellidae, Scythridae, Yponomeutidae, Glyphipterygidae, Heliodinidae, Elachistidae (= Cycnodiidae), Epermeniidae, Argyresthiidae, Acrolepiidae, and Bucculatrigidae contain species that are leaf-miners. A few of these mine in all instars, whereas many mine only in the first instar or even only during part of the first instar. The prolegs are sometimes reduced but apparently never lost in any of the species of these families that have been adequately described. For instance, a Glyphipterigid, *Glyphipterix cramerella* F., that feeds within the seeds of cocksfoot, has the prolegs much reduced and

in the mature larva each bears only a single pair of crochets (Chopra, 1925). In addition, the larvae of a very few species of Tortricidae, Pyralidae, Hesperiidae, Zygaenidae, and Phalaenidae are leaf-miners, usually only in their first instar. In none of these is there any evident reduction of the prolegs.

(ii) *Reduction or Loss of Prolegs in Free-living Larvae.*

Generalisations as to the order in which the prolegs are reduced or lost in free-living larvae have already been made (see p. 507), and it is here only necessary briefly to review the groups in which reduction or loss occurs.

Very nearly all of the free-living larvae that have one or more pairs of prolegs reduced or lost live on grasses, shrubs, and trees; and, with the single exception of the Eucleidae, all belong to highly specialised groups of Macroheterocera that have a tympanum in the adult stage. The most numerous of these are the Geometridae and Phalaenidae. In the Geometridae the first three pairs of prolegs are reduced in the primitive Brephinae and are completely lost in most other groups. When crawling a Geometrid grips the substrate with its legs and then draws its body up to form a loop vertical to the surface. In this way the prolegs of the sixth and tenth segments, which are unusually close together, can quickly be placed immediately behind the legs. The larva then secures its prolegs, detaches its legs, and straightens its body. When it again secures a hold with its legs the process is repeated. This method of crawling may be decribed as looping. Most of the larvae that move in this way are able to cover a given distance more quickly than larvae of comparable size that crawl in the normal way using all pairs of prolegs. Perhaps the most obvious selective advantage to arboreal and shrub inhabiting forms of this type of locomotion is that it enables them more effectively to span gaps and climb from one twig or leaf to another. The looping method of crawling is most developed in the Geometridae, and the three anterior pairs of prolegs are more frequently completely lost in them than in any other family. In this connection it is of interest to note that of all arboreal Macroheterocera the Geometridae are the most successful, both as regards numbers of species and numbers of individuals.

That reduction or loss of the anterior pair or pairs of prolegs is correlated with a change in the method of locomotion is particularly evident from a study of the Phalaenidae. Nearly all Phalaenidae use a looping method of crawling in their first or first two instars. This method of locomotion is the rule even amongst those groups that in their later instars crawl in the normal way and have the first two pairs of prolegs as well developed as the following two pairs. In a great many species the first or first two pairs of prolegs are distinctly smaller than the following, and in a number of species they lack crochets or are altogether lost. Reduction of the first pairs of prolegs is relatively greater in the early than in the late instars, and in those species in which they are lost in the mature larvae no trace of them can be found in the early instars. Ripley (1923) has drawn attention to the fact that in some genera of Acronictinae, Phalaeninae and Hadeninae the prolegs of the third abdominal segment are absent in the first two instars but appear as minute organs at the second moult, and thereafter their size relative to the posterior pairs increases with each moult. The mature larvae of nearly all Erastriinae lack prolegs on the third and fourth segments, or, if these are present on either segment, they are much reduced. The first two

pairs of prolegs are apparently reduced in most Catocalinae, and the first pair is frequently lost. In the mature larvae of some genera of other subfamilies the prolegs of the third and fourth segments or only those of the third are reduced or lost.

Although the first one or two instars of the Phalaenidae are always "loopers", looping is, apart from a very few notable exceptions, a method of crawling not used by the later instars of terrestrial species. For instance, none of the cutworms or their allies are loopers in their later instars. In their early instars these usually remain on their host plants, but after the first or second moult, when the habit of looping is lost and the anterior pairs of prolegs are nearly or quite as large as the posterior, they leave the plant during the day and climb up again each night to feed. The habit of looping is so widespread among the later instars of the species that live on shrubs and trees and is so frequently reflected at a morphological level (reduction or even total loss of some anterior prolegs), that it seems justifiable to conclude that this method of locomotion, and such structural alterations as may in time be evolved in connection with it, are adaptations to a life on twigs or leaves of plants.

The fact that the habit of looping is apparently present in the early instars of all terrestrial and even subterranean Phalaenidae suggests that such species are derived from those that live on plants and that, therefore, the terrestrial or subterranean habit is secondary in the Phalaenidae. This hypothesis seems reasonable when we consider that, although looping does appear to enable the larvae to move more rapidly, its chief selective advantage seems to lie in enhancing the efficiency of the larvae in crawling about on plants. If the advantage of looping were merely a matter of increasing speed we should expect to find the habit of looping evolved in at least some of the terrestrial larvae of other families. In this connection it is interesting to note that of the relatively large caterpillars those of the semi-terrestrial Arctiidae, in which the anterior pairs of prolegs are not reduced, are capable of the greatest crawling speeds. Furthermore, even in their first instar all have the crochets of the prolegs arranged in a mesoseries, which, as has been shown in an earlier section, is an adaptation evolved only in connection with climbing on plants. The Arctiidae are secondarily semi-terrestrial, as is shown by the fact that their prolegs are, in all instars, modified for climbing.

A very large number of Microlepidoptera are arboreal or live on shrubs and grasses. Most of these are not loopers (I know of none that are), but this fact cannot be advanced against the hypothesis that looping is an adaptation to climbing about on plants because the great majority of plant-inhabiting Microlepidoptera live in webs, or in curled or rolled leaves, or in other shelters, and are rarely freely exposed as are the Macroheterocera. Furthermore, they rarely wander about, and during all of their active life they are usually restricted to a single leaf or group of leaves. A further factor that may play a part in their failure to develop the looping habit is the unfavourable relation between their body length and the average size of the gaps between the leaves and the twigs of the large plants on which they live. Among the Geometridae are many small species found on bushy herbs where their shorter reach may to some extent be compensated by the shorter gaps between adjacent leaves and twigs.

The Sphingidae, Saturniidae, Bombycidae, Lasiocampidae, and other large caterpillars that live on shrubs and trees, do not loop and have the anterior

pairs of prolegs as well developed as the posterior. These caterpillars are adapted in another way to an arboreal life. They move very slowly, and their prolegs are unusually well muscled so that their purchase is exceptionally secure. The opening and closing of the prolegs is a complex operation that has not been adequately described. These slow moving groups also attack leaves in a different way. As Tutt (1899) points out, a Geometrid will stretch out to its full length and often eat as much as it can reach without moving, frequently beginning near the tip of the leaf. The more powerful Sphingid, on the other hand, pulls the leaf towards itself, " and does by greater strength what the Geometrid does by greater reach ".

The larvae of the Nolidae have lost the prolegs of the third abdominal segment. A few genera of Notodontidae, e.g. *Gargetta* (Gardner, 1944), have the prolegs of the third and fourth abdominal segments much smaller than the remaining prolegs, or those of the third segment may be lost. Both the Nolidae and Notodontidae are typically arboreal, but some feed on shrubs.

The prolegs of the tenth abdominal segment are noticeably reduced, lost, or modified to subserve functions other than locomotion in a number of free-living larvae that belong to specialised tympanum-bearing families, namely : Drepanidae, Thyatiridae, Syntomidae, and Notodontidae. All of these are arboreal or live on shrubs. Anal prolegs are more or less entirely lost in the Drepanidae. In this family the tenth segment is moderately to greatly produced behind. The larvae are said to " frighten away " enemies by elevating the long tail-like tenth segment or rubbing it to and fro against the leaf surface when they are suitably stimulated. Some of the species of the related family Thyatiridae have the anal prolegs reduced. The reduced anal prolegs are said to be usually more or less raised when the larva is at rest. Many Thyatirids live in loosely rolled or folded leaves. Some Syntomidae are said to have lost the anal prolegs, but I have seen none of these.

The structure of the anal prolegs is very variable in the Notodontidae. In the Notodontini and Nystaleini they may be only slightly reduced and may function in the normal way in crawling. In the Heterocampini they are very much reduced and are apparently non-functional in many species. In some Melalophinae they are well developed and function in crawling but are raised when the larva is at rest, and in some way probably function as defensive organs. In most Phalerinae they are vestigial and without crochets. In the Cerurinae they are mostly very long, and a considerable part of the apex of each is very slender and usually brightly coloured. The slender apices are normally invaginated. When the larva is stimulated they can be suddenly eversed, and all observers are agreed that they function in defence.

The Eucleidae (= Limacodidae, Heterogeneidae) are the only free-living larvae that have no prolegs. Thoracic legs are present but reduced. The larvae live on shrubs and trees and are usually found on the upper surfaces of leaves. Some genera have feebly formed ventral suckers, usually on the first seven abdominal segments. In at least some genera a liquid is secreted over the cuticle. If this is not actually sticky, it may function when they crawl by increasing the efficiency of the suckers or by surface tension binding the abdomen to the leaf surface. I know of no convincing explanation of how these larvae lost their prolegs.

The Megalopygidae, which live on shrubs and trees, are apparently unique

in having two additional pairs of prolegs, one on the second abdominal segment and the other on the seventh, neither of which has crochets.

The Epipyropidae are all ectoparasites of Homoptera. Some writers, e.g. Zerny and Beier (1936) claim that legs and prolegs are absent in the young larvae but are present in the later instars. First instar larvae actively search for their hosts and when they find them remain on their backs until they are full grown. It is therefore extremely improbable that the first instar of any species lacks legs or prolegs. I have only been able to examine the first instar of *Fulgoraecia cerolestes* Tams, and it has both legs and prolegs, the latter being, as might be expected, proportionally larger than those of the inactive later instars.

C. Trichoptera.

The larvae of all Trichoptera have a pair of anal prolegs on the tenth abdominal segment, and not on the ninth, as stated by some. The proleg muscles of a Limnophilid and a Hydropsychid have been figured by Snodgrass (1931, 1935), and a comparative account of the musculature of the prolegs of a number of families has been given by Pryor (1951). In some, e.g. mature Limnophilidae, each proleg consists of a strongly curved claw and two basal sclerotised plates that may be articulated to a sclerotised part of the side of the tenth segment. The degree to which the tenth segment is longitudinally divided varies considerably. Even within one family, e.g. Limnophilidae, the tenth segment may be nearly entire or nearly completely divided. When the tenth segment is deeply divided, as in most families, the whole of one side becomes the basal part of the proleg of that side. For instance, as shown by Pryor, both in the Polycentropidae and Philopotamidae the tenth segment is completely divided and even part of the ninth segment becomes incorporated into the basal part of the terminal appendage or proleg. In many families, e.g. the Limnophilidae, not only are the prolegs frequently relatively larger in the first than in later instars, but the division of the tenth segment is more complete. This fact has given rise to such curious statements as that of Hickin (1946, p. 207), " ... in the Hydropsychidae there is some fusing of the proximal segments of the appendages as the larva develops, with a consequent shifting of the anal opening posteriorly".

Two opinions may reasonably be held as to the nature of the anal prolegs of the Trichoptera. They may be thought to be homologues of the cerci that are still retained by many exopterygote larvae. They may, on the other hand, be thought to be secondary organs as are the ventral prolegs of the larvae of other Panorpoid orders. I hold the latter view but without conclusive evidence for it.

It is not known if cerci were present in the common ancestor of the Panorpoid orders. Trichopterous larvae retain a larger number of primitive features than the larvae of any other order of the Panorpoidea. Since all trichopterous larvae have anal prolegs, it is possible that these are homologues of cerci. If this be so, the form and musculature of the trichopterous appendages has now departed very widely from that of the cerci still retained by many exopterygote larvae. If the prolegs are indeed homologues of the cerci, and therefore according to Snodgrass serially homologous to thoracic legs, it follows that the more complex their structure and the more they resemble thoracic legs the more they have departed from their ancestral form. In other words, irrespective of whether they are primary appendages or provisional larval organs, the more they resemble

thoracic legs the more certain it is that the resemblance is secondary. In some Trichoptera, e.g. Polycentropidae, the prolegs resemble thoracic legs as much as the reduced thoracic legs of the Mecoptera resemble the thoracic legs of the Trichoptera, and it is of interest to note that the claw has both levator and depressor muscles, whereas the claw(s) or pretarsus of the legs (thoracic of hexapods and trunk of myriapods) lacks levator muscles in all members of the subphylum Antennata.

In his comparison of the terminal prolegs of *Corydalus* with those of the trichopterous genus *Rhyacophila*, Pryor (1951 : 357) says, " The fixed hooks correspond in position to the filaments of *Corydalus*, and their relation to the external lateral muscles of segment 10 confirm that they are in fact truly homologous ". The similarity to which Pryor draws attention may be remarkable, but what he concludes from this similarity does not bear close examination. The Megaloptera and Trichoptera are unrelated orders, each of which belongs to a different section of the Endopterygota. These two orders have invaded aquatic environments independently, and, so far as we know, in quite different geological periods. Furthermore, there is no evidence whatever that the terrestrial ancestor of either had terminal abdominal appendages even remotely resembling those of recent Megaloptera and Trichoptera. If the ancestor of either had terminal abdominal appendages, all the available evidence points to these being simple, cerci-like appendages similar to those possessed by many recent Neuropteroidea. It may be noted here that in other aquatic Megaloptera, i.e. Sialidae, the tenth abdominal segment is produced to form a single long filament and there is no trace of the terminal appendages of the Corydalidae. Furthermore, in the only known recent Megaloptera that are terrestrial, i.e. the Raphididae, the tenth abdominal segment is short, rounded, and lacks appendages. These facts suggest that the appendages found in the Megaloptera only in the family Corydalidae are evolved *de novo* and not even from the simple cerci-like appendages present in many terrestrial endopterygote larvae.

Pryor (1951 : 356) accepts the suggestion of Snodgrass (1931) that the terminal appendages of megalopterous larvae are serially homologous with the gill tufts of the same larvae, but points to a difference in the musculature of the two structures. It is important to note that the argument for homology accepted by Pryor is incorrect *in principle*. A similarity of musculature is not necessarily good evidence for suggesting a homology of prolegs with gills or gill tufts as is particularly evident on comparison of (1) the similarly muscled but independently evolved and therefore non-homologous ventral, lateral, and dorsal prolegs of a single abdominal segment of a Tabanid larva or (2) the identical musculature of prolegs independently evolved in many families of Diptera, or (3) the similar musculature of the prolegs of some dipterous and lepidopterous larvae. In this connection it is important to note that a dissimilarity of musculature, however great, between two organs is not certain evidence that they are not homologous. For instance, there is little resemblance indeed between the musculature of the thoracic legs of mecopterous and trichopterous larvae, but few would seriously dispute the fact that the thoracic legs of the larvae of these two orders are homologous. In short, the close resemblance between the terminal appendages of megalopterous and trichopterous larvae is either the result of parallel evolution or convergent evolution from ancestors possessing cerci-like terminal appendages or none at all. Support for this view is to be had from the

Gyrinidae. The aquatic larvae of the Gyrinidae (Coleoptera) have terminal abdominal claws which very closely resemble those of some Corydalidae. The Gyrinidae, however, are a group of Caraboid beetles derived from ancestors that were terrestrial and which probably had simple cerci-like appendages like those of recent primitive Caraboidea.

The attempt by Pryor (*loc. cit.* : 359 *et seq.*) to establish homologies between the individual muscles of the terminal appendages of megalopterous and trichopterous larvae can serve no useful purpose, since such homologies cannot exist between organs that have evolved independently from organs without such muscles or even *de novo*. For similar reasons, the statement by Pryor (*loc. cit.*: 360) that the development of the lateral muscles of the tenth segment as the main flexors of the claw of *Rhyacophila* " . . . has resulted in the *loss* [my italics] of the inner claw found in *Corydalus*, which is remote from the muscle attachments " has no foundation in fact.

D. Zeugloptera and Mecoptera.

In the Zeugloptera and Mecoptera paired ventral prolegs are present only on the first eight abdominal segments. They lack muscles and therefore can only be moved by variations in turgor pressure or indirectly by muscles inserted in the adjacent parts of the sternites. When the larva is at rest on a flat surface they often function as supports that keep the ventral surface of all segments except the ninth (Zeugloptera) or tenth (Mecoptera) from contact with the substrate. In locomotion they secure a purchase for the larva and serve to transmit the thrust of the segments against the substrate.

The absence of muscles in the prolegs of Mecoptera has been previously noted by Applegarth (1939 : 113), who says : " From the ventral side arise the paired appendages which seem to be vestigial legs. Their status is not determinable directly. They have no muscles and if this be considered decisive they would be regarded merely as secondary processes. However, in structure they very closely resemble the apices of the thoracic legs, being transversely wrinkled and bearing rows of minute setae on their outer side. Because of their similarity and because of their position, they are here accepted as vestigial legs."

The musculature of the appendages of two different segments is only a guide in determining their corresponding epidermal parts, and the absence of muscles in the appendage of one segment has no neccessary bearing on the question of its homology with a muscled appendage of another segment. For instance, the pretarsus of the Mecoptera has lost the pretarsal retractor, or, if the homologue is present, it is no longer inserted in the pretarsus, but this fact of itself does not prove that the claw of the mecopterous leg is not the pretarsus. The mecopterous leg is a multi-segmented structure, whereas the proleg is unsegmented, and Applegarth is comparing the whole proleg with only the pretarsus and tibio-tarsus of one of the most reduced larval legs in the Panorpoidea.

E. Siphonaptera.

The larvae of the Siphonaptera have two cylindrical ventral prolegs, the " anal struts " of authors, that arise from the perianal membrane of the tenth abdominal segment. No muscles extend into these prolegs, but some fibres are

inserted on or very near their basal margin, and they also appear to be moved by the muscles inserted in the immediately adjacent perianal membrane. I am not aware that anyone has questioned the fact that they are secondary structures. In external form and the absence of intrinsic muscles they resemble the anal struts or prolegs of the Therevidae.

III. THE BERLESE-IMMS THEORY AND THE STRUCTURE AND DISTRIBUTION OF PROLEGS.

Paired locomotory appendages are present on the ventral surface of the abdomen of many endopterygote larvae. The status of these structures has been a perennial source of dispute. There are those, now in the majority, who claim that those appendages are of the same series as the thoracic legs and that they are the embryonic abdominal appendages of the polypod embryo retained by the larva after hatching. This is the view of all adherents of Berlese's theory or other theories that claim that the larvae of the Endopterygota are precocious embryos rather than definitive larvae.

On differences in the development of the segmental appendages during embryonic growth, it is possible to distinguish three successive phases through which insects normally pass. These are not sharply differentiated, and the embryo gradually passes from one to the other as segmentation proceeds from the anterior to the posterior end. The appendages of the head appear first and are followed by the thoracic and, a little later, the abdominal. The appearance of the abdominal appendages marks the end of the protopod and the beginning of the polypod phase. The polypod phase passes into the oligopod when the abdominal appendages are absorbed. During these embryonic phases development of the other organ systems is continuous.

According to Berlese (1913) and Imms (1937), the forms of the chief kinds of larvae are determined by the time of hatching. They claim that larvae with abdominal prolegs like those of the Lepidoptera, Mecoptera, and saw-flies, have emerged from the egg in the polypod phase, whereas beetle larvae and others that lack prolegs have emerged in a later embryonic phase, the oligopod. The apodous larvae of Coleoptera, Hymenoptera-Apocrita, and Diptera are regarded by them as derived from the oligopod phase by reduction and loss of the thoracic appendages. They claim that the larvae of the Exopterygota, which they call nymphs, have emerged from the egg in a post-oligopod phase, The so-called " primary " larvae of some parasitic Hymenoptera have, according to Berlese and Imms, emerged in the protopod phase. For instance, in the Proctotrypoidea the eggs are almost devoid of yolk and are surrounded by the yolk or haemolymph of their hosts. The primary larva has an unsegmented abdomen, rudimentary thoracic legs, undeveloped nervous and respiratory systems, and its gut is little more than a mesenteric sac.

The theory of Berlese, therefore, postulates two primary categories of larvae : the oligopod or preoligopod and the post-oligopod (nymph). To the first of these categories belong all the forms that are described as " true " larvae and are in fact considered to be precocious embryonic stages by the adherents of the theory. To the second category belong the forms they call nymphs. This theory also implies that in the first category there are two subsidiary but sharply differentiated categories, namely : (1) forms whose chief differences may be

attributed to differences in embryonic growth attained before hatching; and (2) forms derived, but differing in varying degree from the oligopod type owing to adaptive modifications in the direction of simplicity, e.g. apodous larvae.

Supporters of Berlese's theory often claim that it is the relative amount of yolk in the egg that determines the embryonic phase in which the larva hatches, the smaller the amount of yolk in relation to the size of the embryo the earlier the embryonic phase in which it hatches.

No one disputes the fact that the Endopterygota are derived from some group or groups of the Exopterygota and that therefore the ontogenetic sequences of the endopterygotes are derived from those of the exopterygotes. According to Imms (1937 : 63) " . . . the pupa, along with the antecedent prepupa, are the ontogenetic counterparts of the nymphal instars of the lower orders of insects. It seems that tachygenesis, or shortening of development, has resulted to the extent that the whole series of nymphal instars has become concentrated into these two stages, with the elimination of the intervening ecdysis." I have previously (Hinton, 1946*a*) shown that there is no such instar as the prepupa of Imms and Berlese, and I have (Hinton, 1948) dealt in detail with the absurdities inherent in the view that the pupa originates by tachygenesis of the larval (nymphal) instars of the exopterygotes.

The Berlese-Imms theory has been slightly modified by Henson (1946) who points out that the polypod Lepidoptera and Symphyta are definitive larval forms of more complex organisation than the reduced oligopods. To him retention of legs and prolegs is not a criterion of degree of development and he therefore does not consider that the polypod and reduced oligopod larvae stand in the same relationship to one another as the polypod and oligopod embryonic phases. This promising attack on the Berlese-Imms theory is not further developed. Instead, Henson explains differences between larval forms by assuming that they are due to varying degrees of intensity of action by an inhibitor hormone. He concludes his paper as follows: " What has been inherited from the common ancestor of the holometabolous groups is not a particular larval form but the hormone mechanism of growth control. Each order, or even different groups within a single order, have been able to evolve their characteristic larval types by modifications of the hormone mechanism, perhaps nothing more than alterations in the concentration of the suppression factor, or different susceptibility of the different organ systems."

The theory that the ventral abdominal locomotory appendages of the Endopterygota are homodynamous with the thoracic legs has been rejected by Deegener (1909) and others, who claim that the prolegs are secondary or provisional larval organs and are not in the same series as the thoracic legs.

These two theories of the origin of the abdominal prolegs are diametrically opposed. If Berlese's and similar theories are correct, a group in which the larvae have prolegs can be derived from one lacking prolegs only if it constitutes an exception to Dollo's law in respect of these structures. If, however, the prolegs are secondary adaptive structures, there is no *a priori* objection to deriving groups in which the larvae have prolegs from those in which they are absent. For these reasons, therefore, it is essential to come to some conclusion as to the status to be accorded to the abdominal prolegs (larvipods, pseudopods, pedes spurii, *auct.*) if these structures are not to be neglected when discussing the

ways in which the orders of the Panorpoidea are related to each other. Whether the prolegs are secondary structures or whether they are homodynamous with the thoracic legs is critical to many of the arguments of a subsequent paper, and therefore the whole question of prolegs and the theories that maintain that they are segmental appendages in the same series as the thoracic legs are dealt with at greater length than at first sight appears necessary. Oddly enough, there exists no comprehensive account of the prolegs notwithstanding their importance to many generally accepted theories, such as that of Berlese.

The Berlese-Imms theory seeks to explain the chief differences of larval form as due to the relative amounts of yolk in the egg, whereas Henson and others find an explanation in the level of concentration or the intensity of action of an inhibitor hormone. Both theories are characterised by being extremely one-sided. Both attempt to explain major differences of form amongst the very stages of insects that are most intimately and complexly related to their environment by ignoring the effects of the interaction of the larva and its environment. It is not, therefore, surprising that supporters of Berlese's theory should state, as does Imms (1937 : 62), " In the past the tendency has been to overstress the influence of adaptation in determining the evolution of larval forms ". Now, unless the theory of natural selection is to be disputed and some unknown inner force—presumably orthogenetic—is to be put in its place, it is difficult to attribute not only the chief differences in larval form but even relatively minor ones to anything but selected modifications (adaptations) to their environment at some time in their history. The Berlese-Imms and Henson theories fail to give a satisfactory explanation of the continual appearance in any evolutionary line of structures so altered as to be qualitatively different. This difficulty has been perceived by Imms, who deals with it in the following fashion : " Berlese's theory maintains that insect larvae . . . are subject to the same laws affecting other organisms, and, consequently the particular ontogenetic phase exhibited in the species of one group may be largely obscured by secondary features, and yet be plainly evident in another group . . . Berlese's theory co-ordinates and explains the significance of diverse larval types which can only, otherwise, be interpreted as intercalated and purely adaptive phases." In other words, larval types that do not fit the requirements of Berlese's theory are dismissed as being " largely obscured by secondary features ", and, conversely, those that do fit are assumed not to have been subject to the same extent to change through selection during the history of their relations with the environment.

The only part of the Berlese-Imms theory that is accepted here is that which claims that the primary larvae of some parasitic Hymenoptera are precocious embryos. To so regard these primary larvae seems justifiable in view of the fact that eggs of such species are almost devoid of yolk and are surrounded either by the yolk of their host eggs or the blood of their host larvae. Moreover, on hatching the primary larva has an unsegmented abdomen and undeveloped nervous and respiratory systems.

The idea that larvae are precocious embryos is, of course, a very old one. William Harvey explicity stated that it was the lack of food reserves in insect eggs that caused what it pleased him to call premature birth ; and this belief is implicit in the theories of others. Berlese's theory might be described as an elaboration of Lubbock's (1874 : 80) thesis : " That the occurrence of meta-

morphosis arises from the immaturity of the condition in which some animals quit the eggs." According to the Berlese-Imms theory, the food reserves in the eggs of the Endopterygota are inferior in quality or less abundant relative to the size of the embryo than those in the eggs of the Exopterygota, and, as a consequence of this, the former hatch in an oligopod or pre-oligopod embryonic phase and the latter in a post-oligopod phase.

There is, as yet, no proof of any kind that the eggs of the Exopterygota as a whole contain either relatively more yolk or more nutritious yolk than those of the Endopterygota. It has been shown for at least one endopterygote that there is much more yolk in the egg than is required for the embryo. Alston (1923) found that the larva of a beetle, *Lyctus brunneus* Steph., makes its first meal from the residual yolk-mass left in the anterior end of the egg, and, if not interrupted by the observer, will eat all of the yolk before quitting the egg. Although no conclusions can safely be drawn from an isolated instance, the development of *Lyctus* does suggest that its emergence in an " oligopod " instead of a " post-oligopod " form cannot be attributed to the lack of food reserves in the egg.

No comparative studies have been made on the relative sizes of the egg and freshly hatched larva, but the species known to me do not support the theory that the relative size of the exopterygote egg is greater. In this connection it is interesting to note that in one family of beetles, the Histeridae, there are species with oval eggs more than a third as long as the female and others with somewhat flattened eggs less than one-twentieth as long as the female (Hinton, 1945) but the larvae of both are " oligopods ".

From what has been said, it is clear that if it can be demonstrated that the prolegs of the abdomen are secondary structures and not homodynamous with the thoracic legs one of the corner stones of the Berlese-Imms theory will have been removed.

If prolegs are homodynamous with thoracic legs and are therefore " true " segmental appendages we should expect to find that :

(1) Prolegs should more often be retained in relatively primitive than in relatively specialised groups, since no one denies that insects are derived from myriapod-like ancestors that had a pair of appendages on each segment of the trunk (p. 524).

(2) It should not be possible to derive groups with prolegs from those without prolegs or homologous structures (p. 528).

(3) Primary segmental appendages might be retained on the first seven abdominal segments of at least some Exopterygote larvae, since the endopterygotes are derived from some group of exopterygotes (p. 529).

(4) It should not be possible to find many instances of closely related groups amongst which prolegs are present in some genera and species and absent in others, since, according to the Berlese-Imms theory, there is a relatively fundamental difference between them, those with prolegs having emerged from the egg in an earlier embryonic phase than those without prolegs (p. 530).

(5) It should not be possible to show that prolegs have been evolved independently many times (p. 530).

(6) It should be evident from the structure of both primitive arthropods and all recent groups of the phylum that no segment of the body bears more than a single pair of appendages serially homologous with legs. It should, therefore,

follow that should any abdominal segment of an endopterygote larva bear appendages serially homologous with thoracic legs, there can only be one pair of such appendages (p. 531).

(7) When thoracic legs are lost and secondary locomotory appendages are present on the thorax, these secondary larval organs are hardly likely to be identical in structure with the abdominal prolegs if the latter are indeed true segmental appendages and not merely provisional larval organs (p. 531).

(8) The structure of the prolegs of relatively primitive groups, as compared with relatively specialised groups, should more nearly approach the structure of the appendages to which they are said to be serially homologous (p. 531).

(9) During embryonic development there should be some structural discontinuity between the primary abdominal appendages present in the polypod phase and those appendages present in the late oligopod embryos that are retained as functional prolegs in the larva (p. 532).

Each of these propositions is dealt with *seriatim* below.

(1) Prolegs should more often be retained in relatively primitive than in relatively specialised groups, since no one denies that insects are derived from myriapod-like ancestors that had a pair of appendages on each segment of the trunk.

In the Panorpoidea ventral prolegs are present in the Mecoptera, some Diptera, Lepidoptera, and Zeugloptera, but are absent in the Trichoptera and *Boreus*. Of the larvae of the recent Panorpoidea none have retained as many primitive features as those of the Trichoptera, which in some relatively minor respects, such as having an apneustic respiratory system, are highly specialised for aquatic life. That their lack of prolegs is not another of their specialisations for life in the water seems certain from the fact that neither legs nor prolegs are lost by any other insects that have invaded water, but, on the contrary, invasion of water frequently results in the acquisition of prolegs. For instance, in the Diptera prolegs are nearly always present in aquatic species but are nearly always absent in terrestrial forms.

The absence of prolegs in *Boreus* is especially interesting. *Boreus* is in nearly every way very much more primitive than the Mecoptera that have prolegs, and both *Boreus* and proleg-bearing Mecoptera are terrestrial. The Mecoptera and Diptera are closely related orders, but, on balance, the Diptera are, as few will deny, much more specialised. The prolegs of the Diptera are much more developed than those of the Mecoptera, and, moreover, have retractor muscles, which are absent in the prolegs of the Mecoptera. On the Berlese-Imms theory that the Diptera are reduced oligopods, their prolegs have to be reckoned as secondary structures that are not homologous to the prolegs of the Mecoptera.

In the other section of the Panorpoidea, the prolegs of the Zeugloptera and Lepidoptera are structurally related to one another, as are those of the Mecoptera and Diptera. Those who would include the Zeugloptera in the order Lepidoptera nevertheless agree that the Micropterygidae are the most primitive of recent Lepidoptera. Adherents of Berlese's theory claim that the prolegs of caterpillars are homodynamous with the thoracic legs, sometimes drawing attention to presumed similarities between the musculature of the two; and it appears that none of them are aware that the prolegs of the Micropterygidae lack muscles.

In the Neuropteroidea ventral abdominal prolegs are rarely present in terrestrial species, but such structures are borne on the first few abdominal

segments of some Oedemeridae (*Nacerdes*) which no one regards as being particularly primitive. In the aquatic members of the superorder tracheal gills are frequently present. Their position on the abdomen is very variable, as might be expected if they are the secondary adaptive structures I believe them to be. Sometimes, e.g. some specialised Haliplidae (*Peltodytes*), many gills are present on a single segment. The gills of these species are considered to be secondary adaptive structures by Berlese's supporters. However, in others such as the Sialidae, Corydalidae, Sisyridae and Gyrinidae, only a single pair of lateral or ventral gills may be present on most abdominal segments. In the latter groups the gills are no longer secondary structures but are held to be primary segmental appendages homodynamous with thoracic legs by the adherents of Berlese's theory.

Many of those who maintain that the gills of the Neuropteroidea are primary segmental appendages also claim that the larvae that bear them are primitively aquatic and that all terrestrial insects came from aquatic ancestors at some point in their evolution. It is necessary to dispose of this claim in order to develop my thesis that gills are secondary adaptive structures.

One of the chief distinguishing features of the class Insecta is its tracheal respiratory system, which has nine (Machilidae) or ten (Lepismatidae and all primitive Pterygota) pairs of spiracles. Except for a small number of highly specialised parasitic species, the respiratory system of all postembryonic stages of all insects conforms to this basic pattern. Now, unless it be supposed that a tracheal system was evolved in water, its existence in all stages of all insects is proof that the class is a primitively terrestrial one. The insects are the most specialised class of the subphylum Antennata (= Labiata) and the only one in which truly aquatic species occur. It has been shown (Hinton, 1947) that one of the most characteristic and universal structural alterations undergone by insects when they invade water is a reduction in the number of functional spiracles; and, broadly speaking, the degree to which the functional spiracles are reduced is an indication of the degree to which the insect is adapted to life in the water. Keilin (1944) and Hinton (1947) have drawn attention to the fact that any spiracles that become non-functional in any instar of an aquatic insect never return to their functional condition in that instar even though the group may later become wholly terrestrial. In other words, no exceptions are known to Dollo's law so far as the spiracles are concerned. The fact that the spiracles are functional in all stages and instars of the Apterygota and primitive Pterygota that are now terrestrial is therefore further evidence that insects are primitively terrestrial.

The Sisyridae are the only known larval Neuroptera that are strictly aquatic, and they are the only ones that have paired ventral abdominal appendages. A pair of segmented gills is present on the first seven abdominal appendages of *Sisyra* and its allies. According to Withycombe (1925), "*Sisyra* is clearly one of the most highly specialised of all Neuropterous larvae". This is true of both its structure and habits. Of its gills, Withycombe says: "These are somewhat leg-like and suggest true abdominal appendages, but that they are purely secondary is shown by their absence in the first instar." Kimmins (1944), however, claims that gills are present in the first instar. Even if Withycombe's facts are correct, his reasoning is not, since the loss of primary segmental appendages is sometimes confined to one instar. For instance, some of the

leaf-mining Lepidoptera lack thoracic legs in the first but not in the second and following instars. In many other insects marked structural adaptations are confined to one instar or to one stage, since within limits each is selected without reference to those that follow or come before. This differential selection also occurs between organ systems of the same instar or stage of the same species, and therefore the speed of evolution or morphological change is always unequal between species or between organ systems of the same species. The evidence that the gills of *Sisyra* are secondary structures evolved in connection with its aquatic existence, and not primary appendages adapted to subserve a respiratory function, rests on the fact that none of the terrestrial larvae of more primitive groups have paired ventral appendages.

In the aquatic larvae of the Gyrinidae (Coleoptera) and Megaloptera there is a pair of lateral gills on each of the first seven to nine abdominal segments. In this connection it is of interest to note that some Gyrinidae, e.g. *Dineutus*, have two pairs of lateral gills on the ninth abdominal segment. These are almost invariably thought to be primary segmental appendages even by those, who, like Jeannel (*in* Grassé, 1949 : 854), admit that the gills of other beetle larvae are secondary adaptive structures. The Gyrinidae are either a highly specialised off-shoot of a Dytiscid-like stock, or, perhaps more unlikely, an independent development from a pre-Carabid line. There is some morphological evidence that they are merely a highly specialised group of the Dytiscidae and should be accorded no more than subfamily rank within the Dytiscidae. However this may be, there is general agreement that they belong within the superfamily Caraboidea, and that in both their larval and adult stages are more highly specialised for an aquatic life than any other Caraboidea. The fact that not one of the evidently more primitive Caraboids possess paired abdominal appendages[10] seems to be sufficient evidence for believing that the gills of the Gyrinidae are secondary respiratory structures and not primary abdominal appendages adapted for respiration.

The terrestrial Megaloptera (Raphididae) lack prolegs, but all aquatic species (Corydalidae, Sialidae) have a pair of long lateral gills on each of the first seven or eight abdominal segments. In the Corydalidae the gills are usually unsegmented, but in the Sialidae they are very distinctly segmented. The gills of *Sialis* (*S. lutaria* L., *S. fuliginosa* Pictet) are 5-segmented. They not only look like legs, but have two groups of muscle fibres inserted on the base of the second segment. The Corydalidae and Sialidae are, on balance of characters, undoubtedly the most primitive of the recent Endopterygota. For all these reasons, therefore, it is not surprising that those who contend that the paired abdominal appendages of endopterygote larvae, whether locomotory or respiratory, are homodynamous with thoracic legs should seize on the appendages of *Sialis* as proof of their contention. Looking at the matter a little more closely, however, the conclusion that the gills of *Sialis* are secondary appendages can hardly be avoided.

For reasons given in a previous paragraph, (p. 525), it appears certain that all aquatic insects have at some time or another been evolved from terrestrial ancestors. Even if this were not so, it can be shown on evidence derived from the aquatic Megaloptera themselves that they are (1) a secondarily aquatic

[10] Throughout this discussion I am excluding from consideration the terminal abdominal appendages known as cerci or urogomphi (see p. 517).

group, and (2) that *Sialis* with segmented gills is more specialised than the Corydalidae with simple unsegmented gills.

The presence of the primitive number of ocelli, i.e. three, in the adults of the Corydalidae, together with their simple tarsi, suggests that they are more primitive than the Sialidae, which lack ocelli and have the fourth tarsal segment strongly bilobed. This view is supported by the structure of their larval respiratory systems. It has been shown (Hinton, 1947) that, " In a broad general way, the degree to which the functional spiracles are reduced is an indication of the degree to which the larva is adapted to life in the water ; and the success with which this rule may be applied varies directly with the degree of genetic relationship of the groups being compared, providing only that these have essentially the same habits in the water ". Among the Corydalidae, *Archichauliodes* is in many respects the most primitive. Its larvae are peripneustic in their final as well as early instars. Furthermore, *A. diversus* Walk. of New Zealand has the habit of leaving the water to moult and returning again at the conclusion of each moult (Hamilton, 1940). If this habit is not unique among aquatic insects, it certainly is unknown among those that have gills, and it does show, together with the constant peripneustic system, that *Archichauliodes* is not as specialised for life in water as are the other known aquatic Megaloptera. *Corydalis* is apneustic in its early instars but peripneustic in its final instar. In addition to lateral gills of the first eight abdominal segments, it has tufts of tracheal gills on the ventro-lateral side of the first seven abdominal segments. According to Riley (1873), the ventral tufts of gills are absent in the first instar. Their absence at this time, when the relation of surface area to volume is much more favourable for cutaneous respiration, is not altogether surprising. Some Lepidoptera (Pyralidae), with similar tufts of gills in later instars, also lack them in the first instar. The Sialidae lack ventral gills, but the tracheal system of the final instar is even more reduced, the spiracles of the eighth abdominal segment being non-functional. In view of the facts cited above, I doubt if anyone will deny that the segmented gills of *Sialis* are derived from the unsegmented type of *Archichauliodes* with which they are clearly homologous.

Snodgrass (1935) and Chen (1946) claim that the lateral gills of *Corydalis* are homologues of the styli of Thysanura, whereas the ventral tufts of gills are homologous with the eversible vesicles of the latter. It appears from their work that this claim is advanced in good faith.

In the Hymenoptera paired ventral prolegs are present in many Symphyta but are apparently always absent in the Apocrita except in the early instars of some parasitic species that have proleg-like structures. Whatever view is taken of the status of prolegs, their general absence in the latter suborder is only to be expected since their larvae are either immobile, or nearly so, or are parasitic and even their thoracic legs are secondarily lost.

Benson (1938) and others have shown, on the basis of adult structure, that in the Symphyta the superfamily Megalodontoidea is the most primitive. Within this superfamily the larvae of the Pamphilidae (I have not seen larvae of the Megalodontidae, which are said to be very similar to the Pamphilidae) are apparently the most primitive. Their mouth-parts are as generalised as those of any Symphyta and they have 7-segmented antennae, 5-segmented thoracic legs, and 3-segmented cerci. In apparently only one particular are they more specialised than members of other superfamilies : their metathoracic spiracles

are non-functional, whereas both the Cephidae and Siricidae are holopneustic. The larvae of the three families of the Megalodontidae are free-living. Those of the Pamphilidae and Megalodontidae lack prolegs, which are present on segments 1–10 of the abdomen of the more specialised Xyelid larvae in which cerci are lost. Apart from the Xyelidae, prolegs are absent in all other superfamilies of the Symphyta except the Tenthredinoidea (*sensu* Benson), where they are present, except in some Pergidae, on segments 2–6, 2–7, or 2–8 and also 10. Nearly all workers agree that the Tenthredinoidea are the most specialised Symphyta.

(2) It should not be possible to derive groups with prolegs from those without prolegs or homologous structures.

Most metazoan animals are insects, and amongst these there is no known instance of the subsequent development of an organ of even moderate complexity that has at one time been lost during evolution. In other words, there is no known exception to Dollo's law so far as complex structures are concerned, although certain possible exceptions have been noted concerning very simple structures, such as setae (Hinton, 1946). Ontogenetic sequences sometimes provide what at first sight appear to be exceptions to this rule. For instance, the absence of legs in one instar and their presence in a subsequent larval instar of the same species. Looking at the matter a little more closely, however, instances such as the latter are to be interpreted as exceptions to the law of recapitulation resulting from the selection of adaptive features which obscure, or altogether replace, the expected recapitulative sequences. A clear exception to Dollo's law would be established if it could be shown that some group that had lost thoracic legs in the first instar larva had subsequently given rise to a group that possessed these structures in the first instar. For similar reasons the absence of legs in larval Diptera and their subsequent development in adult Diptera does not constitute an exception to Dollo's law quite apart from the fact that the imaginal buds of the legs are present in the larva.

The possession of abdominal appendages in the polypod phase of insect embryos can be interpreted as the recapitulation of a basic feature of the myriapod-like ancestors of all insects. If prolegs were homologues of these appendages and therefore serially homologous with the thoracic legs, their absence in endopterygote larvae might be interpreted as a loss resulting from an adaptation to the environment. But once lost in the late embryo and the postembryonic larval stages of primitive groups, their subsequent development in the corresponding stages of more specialised groups would in each instance constitute an exception to Dollo's law. As I have shown in section " (1) ", all terrestrial groups with prolegs are clearly derived from groups without these structures. Gills of aquatic larvae are generally held to be homologues of prolegs and therefore serially homologous with thoracic legs. Nearly all groups that have them can be derived from groups that lack them, the only exceptional group in this respect being the Megaloptera. In section " (1) " I have already discussed the strong and detailed evidence for the view that the gills of megalopterous larvae are secondary adaptive structures.

If prolegs are serially homologous with thoracic legs it is necessary to accept the fact that (1) they constitute the only known exceptions to Dollo's law; (2) they are very numerous exceptions to the law, e.g. at least 27 in the Diptera alone; and (3) not a single group is known in which the presence of prolegs does not constitute an exception to Dollo's law.

(3) Primary segmental appendages might be retained on the first seven abdominal segments of at least some exopterygote larvae, since the endopterygotes are derived from some group of exopterygotes.

The derivation of the endopterygotes from exopterygotes is not seriously disputed by anyone, although a few consider that the endopterygotes are a polyphyletic group. For instance, Handlirsch (1908, 1926) and Zeuner (1933) believe that the Coleoptera are independently derived from the Protoblattoidea, a belief based on slight evidence and now completely discredited, chiefly as a result of detailed comparative studies on the anatomy of recent orders. However this may be, if the prolegs of endopterygote larvae were primary segmental appendages, they would be expected to occur in the larvae from which endopterygote larvae were derived. For this reason if it can be shown that at least on the first seven abdominal segments of exopterygote larvae there are no primary appendages, a strong case will have been established for regarding any appendages on the first seven abdominal segments of endopterygote larvae to be secondary adaptive structures. The strength of such a case rests, of course, on the degree of improbability attributed to the possibility of exceptions to Dollo's law.

Only the first seven abdominal appendages are specified to avoid confusion because exopterygote larvae have on the eighth (male) or eighth and ninth (female) the gonopods that are regarded by nearly all as primary appendages serially homologous with thoracic legs. Nevertheless, it can be shown that where prolegs are present on the eighth and ninth segments of endopterygote larvae they are neither the same structures nor the precursors of the gonopods later developed in the pupa and imago.

Of the eight wings now known from the lowermost part of the Upper Carboniferous, some clearly belong to the Palaeodictyoptera and the others to a group apparently ancestral to both the Protoblattoidea and Protorthoptera. The occurrence of distinct orders of Pterygote insects by the beginning of the Upper Carboniferous is ample evidence that by this time winged insects had already a fairly long evolutionary history. The Protorthoptera and the Protoblattoidea are terrestrial insects, and there is no evidence that their ancestors were not also terrestrial. It has generally been supposed, however, that the Palaeodictyoptera had aquatic larvae, and, as they are on balance believed to be more primitive than the other early Upper Carboniferous insects mentioned, their supposed aquatic larvae had been used as evidence that Pterygote insects are primitively aquatic. Handlirsch maintained that the larvae of the Palaeodictyoptera were freshwater forms provided with gills, a contention based, like his theory of the Trilobite origin of winged insects, on a singular lack of evidence. Nevertheless, many workers, e.g. Jeannel (*in* Grassé, 1949), are convinced that the larvae of the Paleodictyoptera were aquatic even though they reject his theory of the Trilobite origin of winged insects.

In a previous section (p. 525) I have cited the chief reasons why insects cannot be regarded as anything but primitively terrestrial without going into somewhat less substantial evidence, such as is provided by their uricotelic metabolism. There is no fossil evidence of any kind for believing that the Paleodictyoptera are aquatic, and, even if they were, we would, on evidence previously cited, have to assume that they were derived from terrestrial ancestors. Lemche (1940) has drawn attention to the fact that, according to the figures given by Handlirsch (1908), the proportion between fossil larvae and

adults of the Palaeodictyoptera is as 1 : 29 whereas in the Blattoidea it is as 1 : 8. We may reasonably assume that the chances of freshwater forms being fossilised are greater, so that, in the absence of any evidence to the contrary, these figures are some slight evidence for the view that the larvae of the Palaeodictyoptera were at least as terrestrial as those of the Blattoidea.

From the evidence summarised in the two preceding paragraphs, as well as on p. 525, it seems to be evident enough that not only are insects a primitively terrestrial group but that the various exopterygote orders are derived from terrestrial and not aquatic ancestors. It would therefore seem that the gills of the larvae of mayflies are secondary adaptive structures and not primary segmental appendages in the same series as the thoracic legs. In this connection it may be noted that in mayfly larvae the gills frequently do not appear until after the first or later moults. The styli of some Thysanura also only appear after the first moult, and there is no good evidence that these are not also secondary organs. In his recent attempt to homologize the abdominal gills of mayfly larvae with the styli of Thysanura, Snodgrass (1954) fails to produce any evidence that requires serious consideration.

It thus appears that in none of the postembryonic stages of any exopterygote order are primary segmental appendages present on any of the first seven abdominal segments. If so, it seems to follow that such organs cannot be present in the postembryonic stages of the Endopterygota, which are derived from the Exopterygota.

(4) It should not be possible to find many instances of closely related groups amongst which prolegs are present in some genera and species and absent in others, since, according to the Berlese-Imms theory, there is a relatively fundamental difference between them, those with prolegs having emerged from the egg in an earlier embryonic phase than those without prolegs.

In the sections on the Lepidoptera (pp. 507–517) and Diptera (pp. 465–499) numerous examples are given of genera with well-developed prolegs that are closely related to genera lacking prolegs. It has also been shown that some genera include species with and species without prolegs. Perhaps the most striking of the latter is the Muscid genus *Phaonia* (see p. 498). Most of the species of *Phaonia* are terrestrial, and these apparently never bear prolegs. A few species in various parts of the world have invaded aquatic environments, and each of these has evolved conspicuous prolegs.

According to the Berlese-Imms theory, those forms with prolegs emerged from the embryo in an earlier embryonic phase than those without prolegs. If this theory were correct it should be possible to show that some difference also existed in the organisational level of other organ systems, since a relatively fundamental difference in the degree of differentiation between those with and without prolegs is postulated by the theory. However, careful comparison of many proleg-bearing larvae with closely related species that lack prolegs does not reveal any difference in the degree of differentiation or organisational level of the various organ systems.

(5) It should not be possible to show that prolegs have been evolved independently many times.

Among the Insecta no group is known that has thoracic legs in a particular instar and is yet derived from a group that lacks thoracic legs in the same instar. In other words, so far as the thoracic legs are concerned there is no evidence of

their independent origin within insects. But this is not true of the prolegs. In the section on the Diptera (p. 461) it is shown that prolegs have been evolved independently in no less than 27 groups of this order, each of these groups being derived from ancestors lacking prolegs in all larval instars. It therefore seems clear that the prolegs of dipterous larvae are secondary adaptive structures. Not only this, but it has been possible to define with some accuracy the physical attributes of the particular environment in which dipterous larvae (but not those of other endopterygote orders) nearly always evolve prolegs as they become more and more adapted to it.

(6) It should be evident from the structure of both primitive arthropods and all recent groups of the phylum that no segment of the body bears more than a single pair of appendages serially homologous with legs. It should, therefore, follow that should any abdominal segment of an endopterygote larva bear appendages serially homologous with thoracic legs, there can only be one pair of such appendages.

Certain dipterous larvae, e.g. some Ptychopteridae, Tabanidae, and Asilidae have more than one pair of prolegs on some abdominal segments; and some of these additional pairs of prolegs may even be on the dorsal side. Since those writers who maintain that prolegs of endopterygote larvae are homodynamous with legs never seek to account for the numerous larvae that have more than one pair per segment we can only suppose that they would maintain that only one of the ventral pairs are segmental appendages homologous with legs, whereas all other pairs are secondary adaptive structures. Against such a view, however, is the obvious identity of basic structure of both dorsal and lateral prolegs with all ventral prolegs (see figs. 12–15), an identity that requires an explanation if among the prolegs are included organs of two quite different phylogenetic histories.

(7) When thoracic legs are lost and secondary locomotory organs are present on the thorax, these secondary larval organs are hardly likely to be identical in structure with the abdominal prolegs if the latter are indeed true segmental appendages and not merely provisional larval organs.

In many endopterygote larvae thoracic legs are lost. In some of these ventral thoracic prolegs are present. Such thoracic prolegs are secondary adaptive structures. They are neither vestigial thoracic legs nor precursors of thoracic legs, nor, so far as I know, are they considered as such by anyone. Some dipterous larvae, e.g. some Syrphidae and Ceratopogonidae, bear a pair of prothoracic prolegs that do not differ either in appearance or internal structure from the abdominal prolegs, which is hardly to be expected if the abdominal prolegs are phylogenetically much older structures that are homologous with legs.

(8) The structure of the prolegs of relatively primitive groups, as compared with relatively specialised groups, should more nearly approach the structure of the appendages to which they are said to be serially homologous.

Since the most specialised groups are, by definition, those that have departed most widely from the ancestral type, we should frequently expect to find that the specialisation of these groups also extends to the structure of the legs; and it will be shown in a later paper that as the various organ systems of the larvae become more and more specialised the structure of their legs also departs more and more widely from the primitive type. If the abdominal

prolegs were segmental appendages homodynamous with legs we should expect to find that the prolegs of primitive groups were more like the ancestral leg than those of specialised groups. The opposite, however, is the case. It is precisely those groups that are most specialised that have prolegs that bear a superficial resemblance to legs, whereas prolegs are either absent in primitive groups, or, if present, do not bear even a remote resemblance to thoracic legs. For instance, compare the prolegs of one of the primitive Monotrysia with those of one of the highly specialised Ditrysia, e.g. the lobster-moth caterpillar.

(9) During embryonic development there should be some structural discontinuity between the primary abdominal appendages present in the polypod phase and those appendages present in the late oligopod embryo that are retained as functional prolegs in the larva.

It would seem at first sight unlikely that the prolegs are secondary adaptive structures if it can be shown that during embryonic growth they arise by direct transformation of the appendages of the polypod embryo. According to Friedmann (1934)[11] and many earlier embryologists, the prolegs of such Lepidoptera as have been studied (all higher Ditrysia) develop directly from the primary appendages of segments 3–6 and 10 of the polypod embryo, the appendages of the remaining segments being absorbed before the development of the embryo is completed.

The development of the prolegs has not been followed in the Zeugloptera or Mecoptera. The Diptera no longer pass through a polypod embryonic phase, and there is therefore no embryological evidence for the view that the prolegs, which arise in the late embryo of some species, are not secondary structures. Outside the Panorpoidea the prolegs of some Symphyta apparently develop directly from the appendages of the polypod embryo, as do those of the Lepidoptera.

It seems to be beyond dispute[12] that (1) the epidermis of the abdominal appendages of the polypod embryo proliferates to form the prolegs retained by the larva; and (2) that, at least in some species, there is no temporal discontinuity between the growth of some of the abdominal appendages of the polypod embryo and their subsequent growth and transformation into functional prolegs.

It thus seems clear from embryological evidence, as usually interpreted, that in both the Lepidoptera and Symphyta the prolegs are serially homologous to the thoracic legs. Since this conclusion is, as shown in sections "(1)" to "(8)", directly opposed by a wealth of evidence derived from other sources, the interpretation of the embryological evidence must be re-examined.

Whatever view may be taken as to the homology of the epidermal part of the prolegs, it is evident that their muscles are either displaced or otherwise modified abdominal muscles (fig. 23), or are neo-formations, as are most of the proleg muscles of the higher Ditrysia, e.g. see fig. 3. The muscles of the prolegs, as distinct from their epidermal parts, are therefore in no sense homo-

[11] Friedmann (1934) has published an extensive summary of the embryological evidence for the belief that prolegs of caterpillars are serially homologous to thoracic legs, and the reader is referred to her paper for references to earlier work on this subject.

[12] It must be remembered that there is no experimental embryological evidence either for or against these apparent facts.

logous with the muscles of the trunk appendages of the myriapod-like ancestor of the Insecta and for the same reason are not serially homologous to the muscles of the thoracic legs. There is no comparison either in number or arrangement of proleg and leg muscles in primitive Lepidoptera. The number of proleg muscles increases during the course of evolution, and in specialised arboreal forms may be as great or greater than the number of leg muscles, but their arrangement is always very different (*cf.* fig. 31).

There is, as is well known, a relation between the phylogenetic age of a structure and the time of its appearance in embryogenesis: usually the greater its age the earlier is its appearance. For instance, the tracheal system has been evolved more recently than the legs and in embryogenesis it appears after them.

The prolegs of segments 3–6 and 10 of the Lepidoptera are of great phylogenetic age. They can hardly have been evolved later than the middle Cretaceous and may be much older. Their great age suggests a possible explanation of the lack of discontinuity between the formation of the primary abdominal appendages of the polypod embryo and the development of secondary appendages in the same position on the sternites of some segments.

We may suppose that shortly after the prolegs were evolved they first developed in the late embryo after the absorption of the primary appendages. As their phyletic age increased they appeared earlier and earlier in embryogenesis until there was no longer a hiatus between the maximum growth of the primary appendages and the initiation of the epidermal proliferation that comes to an end when the prolegs are completed.

If the interpretation of the significance of the embryogenesis of the prolegs given in the preceding paragraph is correct, it resolves the apparent contradiction between the evidence cited in sections "(1)" to "(8)", which most strongly suggests that prolegs are secondary adaptive structures, and the particular interpretation of the embryological facts that has been used by others in an attempt to prove that the prolegs of caterpillars are primary segmental appendages.

IV. SUMMARY.

1. The musculature and distribution of the prolegs of the larvae of the super-order Panorpoidea are described.

2. It is shown that prolegs have been independently evolved at least 27 times within the order Diptera.

3. Amongst the Diptera prothoracic prolegs are present only in phytophagous or saprophagous species and never in carnivorous ones except in some chironomidae.

4. It is shown that retractile, crochet-bearing prolegs tend to develop only in dipterous larvae that are aquatic or subaquatic. Evidence is provided that with very few exceptions the terrestrial species that have prolegs are evolved from aquatic forms.

5. An account is given of the reduction of prolegs in leaf-mining and free-living caterpillars. The probable causes of such reductions are discussed.

6. It is shown that the ventral and anal prolegs of the abdomen of lepidopterous larvae have been independently modified to form climbing organs probably no less than eight times.

7. It has been shown that the ventral abdominal prolegs are in each order of the Panorpoidea secondary adaptive structures not serially homologous with thoracic legs. In each order they have arisen independently, and for this reason those of one order are not homologous with those of another, however much they may resemble each other both in outward form and musculature, e.g. those of some Lepidoptera and Diptera.

8. In the more primitive orders ventral prolegs are either absent (Trichoptera, *Boreus*) or lack muscles (Zeugloptera, Mecoptera), and it is only the two most highly specialised orders (Lepidoptera and Diptera) that have muscled prolegs that play a very significant part in locomotion.

9. The balance of evidence suggests that the anal prolegs of the Lepidoptera and Trichoptera are not homologous. There seems to be little doubt that the anal prolegs of the Lepidoptera are not serially homologous with thoracic legs.

10. There appears to be no good evidence either for or against the view that the anal prolegs of the Trichoptera are homologous with anal cerci. But whether they are neo-formations or modified anal cerci, the more complex their structure and the more they come to resemble thoracic legs, the more they have departed from their ancestral form.

11. It is shown that the similarity of structure between the anal prolegs of the Trichoptera and Megaloptera (Corydalidae) is due to convergence or parallelism and is entirely secondary irrespective of whether in one or both orders these prolegs are neo-formations or modified anal cerci. There can, therefore, be no question of homologies existing between the intrinsic muscles of the prolegs of the two orders, as has been claimed by Pryor and some others.

12. The Berlese-Imms theory of development is reviewed. One of the corner stones of this theory is the belief that the abdominal prolegs of various Endopterygota are serially homologous with thoracic legs. The evidence for and against this view is examined in some detail, and it is concluded that in all Endopterygota the prolegs are secondary structures not in the same series as the thoracic legs.

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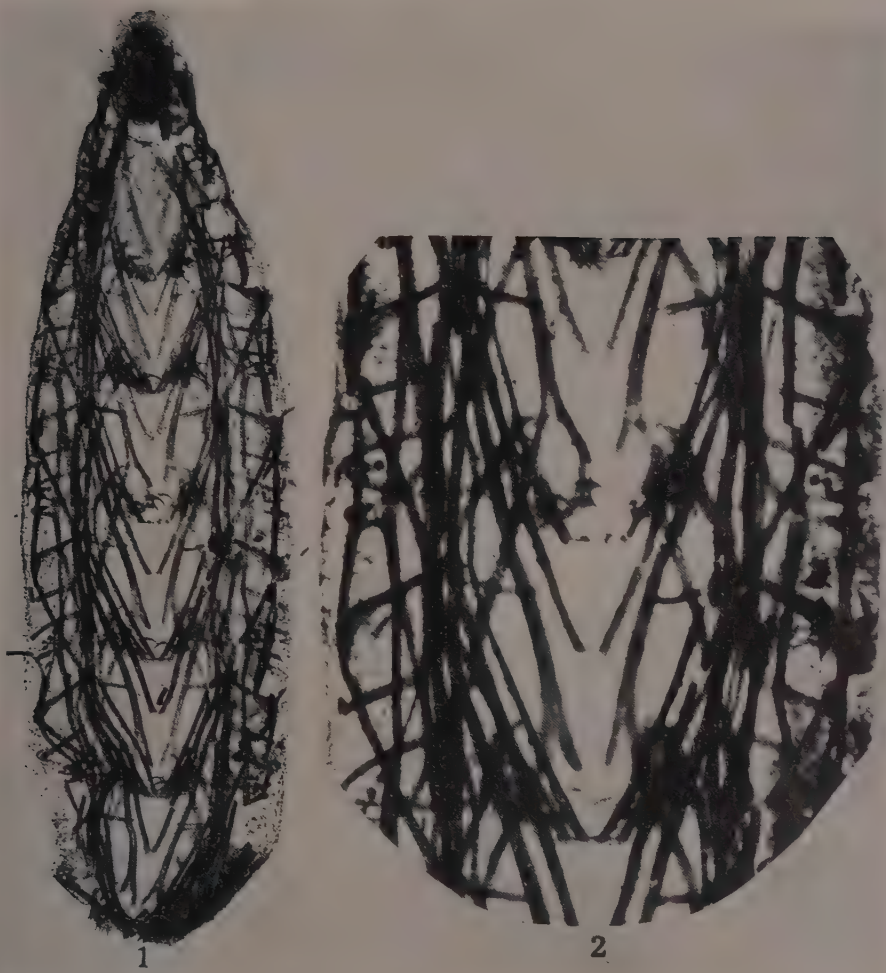
PLATE I.

Figs. 1–2.—*Ephydra riparia* Fallén, mature larva. Dissection of the skeletal muscles of the ventral two-thirds of the larva with most other tissues removed. (1) Thorax and first six abdominal segments. (2) Fourth abdominal segment with part of third and fifth segments. The principal retractor of the proleg of one segment arises near the anterior margin of the segment in front so that this retractor extends through two segments.



Ephydra riparia.

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